

GENETIC AND CYTOLOGICAL OBSERVATIONS IN PRIMARY AND
SECONDARY TRITICALE (X *TRITICOSECALE*, WITTMACK) IN RELATION
TO FERTILITY AND RESISTANCE TO HESSIAN FLY (*MAYETIOLA*
DESTRUCTOR, SAY)

By

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And he gave it for his opinion that whoever could make two ears of corn or two blades of grass to grow on a spot of land where only one grew before, would deserve better of mankind, and do more essential service to humanity, than the full race of politicians put together.

— Jonathan Swift

This dissertation is dedicated to

Robert D. and Elsie E. Martens, my dad and mom,

and

Miss Monica L. Curry, my fiancée,

without whose support and encouragement
this would not have been possible.

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in
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TO FERTILITY AND RESISTANCE TO HESSIAN FLY (*MAYETIOLA*
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By

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The Hessian fly (*Mayetiola destructor*, Say)(Diptera: Cecidomyiidae) is the most important insect pest of wheat and triticale in the Southeast United States. Of the sixteen identified Hessian fly biotypes, E and G composed 83 to 95% of the 1993 populations in northwest Florida. This research was conducted to identify those primary triticale lines which were sufficiently fertile and genetically stable to transfer Hessian fly resistance to adapted triticale; and to identify the Hessian fly resistance allele(s) carried by the tetraploid wheat (*Triticum turgidum* L.) CI 14908. The predictability of transferring Hessian fly resistance from this tetraploid wheat line to triticale was evaluated by screening primary triticale (CI 14908/ Florida 401) and three triticale hybrids derived from crossing biotype E resistant primary triticales with susceptible secondary triticales. F₂ and F₃ bulk populations derived from the primary X secondary hybrids were also screened. Higher

than expected levels of susceptibility were observed. No simple Mendelian genetic model could be determined using population resistance data. Cytological studies were conducted to determine the degree of aneuploidy among primary triticales. Among lines, 5 to 64% of developing C₃ microspores contained unpaired univalents at diakinesis. Pollen stainability, fertility, and further cytological studies were conducted on additional primary triticales lines. Heterogeneity for pollen stainability and fertility, as well as segregation for other traits within lines, suggested that many of these lines may have outcrossed and may no longer be primary, but secondary triticales. Progeny from 10 primary triticales plants grown in the greenhouse in 1995 and 81 secondary plants grown in the greenhouse in 1994 were screened for resistance to Hessian fly biotype L. None of the primary lines were homozygous resistant although several of the secondary lines were. Allelic studies were conducted to identify the loci coding for resistance to Hessian fly biotype E in CI 14908. CI 14908 did not have common alleles with durum wheat lines known to carry resistance alleles H₁₀, H₁₁, H₁₂, H₁₄, H₁₇, H₁₉⁺, and H₂₀, but may have common alleles with lines carrying H₆, H₉, H₁₅, H₁₆, or H₁₈⁺. CI 14908 may also contain alleles not previously reported.

INTRODUCTION

Knowledge of inheritance of resistance to major diseases and pests is important to plant breeders. Plant breeders have been striving for decades to produce cultivars of food and fiber crops that maximize profits, food safety, quality, and aesthetic value while minimizing inputs. Additionally, current political and economic pressures demand that agriculturalists use fewer chemicals while maintaining an abundance of high quality agricultural products. In order to meet these demands, new crops and higher yielding, pest resistant cultivars of current crops must be developed.

Triticale is an amphidiploid cereal grain species developed by intergeneric hybridization of tetraploid wheat (AABB) (*Triticum turgidum* L.) and diploid rye (RR) (*Secale cereale* L.). This is accomplished by embryo culture and colchicine doubling of chromosomes in amphihaploid plants (ABR) (Immonen, 1993; Leley and Gimbel, 1989). The resulting amphidiploids (AABBRR), or primary triticales, vary greatly in fertility for a number of self-pollinated generations. Secondary triticales, by definition, are the progeny produced from primary by primary, primary by secondary, or secondary by secondary hybrids. Secondary triticales form the basis of world triticale production, although some successful primary octoploid triticales [hexaploid wheat (AABBDD) X diploid rye (RR)] have been developed and used in China (National Research Council, 1989). Many primary triticales may never recover good fertility making crossing with another triticale, primary

or secondary, necessary. Shriveled seed and poor vigor are also common in primary triticale, particularly in early generations (Appels and Moran, 1984). Despite the presence of the rye genome (rye is a cross-pollinating species) triticale is generally assumed to be a self-fertilizing species in breeding programs. Early generations of secondary triticale, derived by primary by primary or primary by secondary crosses, commonly have similar problems with fertility and seed shriveling, although typically less severe than primary triticale. Secondary triticale by secondary triticale crosses result in the fewest fertility problems. These characteristics are probably due to varying degrees of aneuploidy and accumulation of deleterious alleles, in addition, rye self-incompatibility genes may also be partially responsible for triticale infertility. One report from the International Center for Maize and Wheat Improvement (CIMMYT) suggested that seed shriveling may also be reduced by a decrease in heterochromatin of the rye chromosomes and possibly the deletion of some rye loci (Skovmand et al., 1984). Other studies on smooth seeded triticale CN605 detected no significant reduction in heterochromatin relative to other triticale lines (Appels and Moran, 1984).

Agronomically, triticale is similar to wheat and subject to similar but not entirely the same limitations (National Research Council, 1989). These limitations include susceptibility to disease and insect pests such as the Hessian fly [*Mayetiola destructor*, Say (Diptera: Cecidomyiidae)]. The Hessian fly has been reported to reduce forage yield of wheat by up to 46% (Buntin and Raymer, 1989a). Since triticale is sometimes grown as a forage crop in the southeastern United States, the potential exists for severe Hessian fly outbreaks. Forage crops of susceptible triticale and wheat may also

act as a reservoir of Hessian fly that can then infest nearby wheat or triticale fields planted for grain production, which are usually planted later than forage plantings. Although the majority of triticales include the entire genome of the rye parent, triticales are often more susceptible to some pests and may not be as vigorous as rye grown in poor soils.

The warm climate of the southeastern United States allows potentially severe epidemics of the Hessian fly (Buntin and Bruckner, 1990). Up to six generations year⁻¹ may occur in this region (Buntin and Chapin, 1990). The Hessian fly is generally considered the major insect pest of wheat and triticale in the southeastern United States and has been an important pest of wheat in North America since the late 18th Century A. D. (Anonymous, 1788; American Philosophical Society, 1792; Lidell and Schuster, 1990; Packard, 1880). The Hessian fly is thought to have been introduced into North America in straw used for bedding, brought by mercenary Hessian troops during the Revolutionary War. These troops landed on Staten and Long Island in present day New York state, August, 1776 (Great Britain Army, 1778).

Damage caused by the Hessian fly during fall infestations usually cause death of the stems fed on by larvae. Damaged stems are weak and winter-kill easily. Spring infection may also cause stem death but more often causes severe stunting or lodging shortly before harvest when heads are heavy with grain (Foster et al., 1986). Sixteen Hessian fly biotypes (designated A to O, and GP) have been identified (Gallun, 1977). A number of control methods have been attempted including seeding dates and other cultural, chemical, and biological controls. Seeding date control can be quite effective in northern latitudes when planting occurs during fly free dates (after killing frosts). Control

by seeding date is ineffective in the southeastern United States because no "fly free date" can be identified in typical years. In this region, the most effective means of control is by the use of genetic resistance.

Gene-for-gene relationships between the host and avirulence in the insect have been demonstrated (Hatchett and Gallun, 1970). Twenty-six "loci" have been discovered to confer resistance to the Hessian fly in wheat, rye, and a wild relative of wheat *Triticum tauschii* (Coss.) Schmal. The loci have been given the designation of H_1 - H_{26} . The loci H_3 , H_5 , H_6 , H_9 , H_{10} , H_{11} , H_{14} and H_{15} have been reported as being located in the A genome, common to both wheat and triticale (Patterson and Gallun, 1977; Patterson et al., 1988; Roberts and Gallun, 1984; Maas et al., 1989; Stebbins et al., 1982; Weller et al., 1991). Locus H_{20} is located in the B genome, also common to both wheat and triticale, while loci H_{12} , H_{17} , H_{18} , and H_{19} have been determined to be located in either the A or B genomes but not to a specific linkage group or chromosome (Amri et al., 1990a; Maas et al., 1987; Obanni et al., 1988, 1988; Patterson et al. 1988; Weller et al., 1991). Most of the remaining loci identified as conferring resistance to Hessian fly (H_7 , H_8 , H_{13} , H_{22} , H_{23} , H_{24} , and H_{26}) are located in the D genome of hexaploid wheat (Amri et al., 1990b; Cox and Hatchett, 1994; Gill et al., 1987; Raupp et al., 1993). Hexaploid triticale does not contain the D genome of hexaploid wheat. The h_4 locus is the only locus known to confer Hessian fly resistance with recessive alleles (Suneson and Noble, 1950). The genomic location of loci H_1 , H_2 , and h_4 is unknown. The H_{21} and H_{25} Hessian fly resistance loci are located in the R genome of Chaupon and Balbo rye, respectively, and have been introduced into hexaploid wheat via wheat-rye chromosomal translocations and subsequent cross pollination (Friebe et al., 1990, 1991; Sears et al., 1992).

United States Department of Agriculture surveys conducted from 1989 through 1992 have indicated that two biotypes, E and G, composed 83 to 95% of the Hessian fly populations in northwestern Florida (Ratcliffe et al., 1994). From 1986 to 1992, a "super-race" of Hessian fly, race L, became predominant in populations sampled in Arkansas, Illinois, Maryland, Missouri, and Mississippi. Race L can only be identified as being virulent to all wheat lines used as differentials and therefore race L may be more genetically variable than other identified biotypes. Screening triticale and hexaploid wheat experimental lines for race L is now a priority for the University of Florida small grains breeding effort.

The primary objective of this research was to identify those primary triticale lines which were sufficiently fertile and genetically stable, to be used to transfer Hessian fly resistance to adapted secondary triticale and wheat lines. A secondary objective was to identify the Hessian fly resistance gene(s) carried by CI 14908.

MATERIALS AND METHODS

Classical Genetic Studies

A number of primary triticale lines were developed by crossing tetraploid wheat and rye (CI 14908/Florida 401 rye, CI 14908/GA-Wren's Abruzzi rye, CI 14432/Syn-T tetraploid rye, and Swan 's/Florida 402 rye) and then doubling the chromosome number in the resulting amphihaploid with colchicine. The primary triticale development was done by Dr. Stanislaw "Maria" Rogalska Department of Genetics and Plant Breeding, Agriculture Academy Poznan, Poznan, Poland in 1989 and 1990 in Poznan and Quincy, Florida. CI 14908 tetraploid wheat (*Triticum turgidum* L. durum group) is a germplasm source of resistance to Hessian fly biotypes C, E, and L. Swan 's' tetraploid wheat originated from CIMMYT and has also been reported to have Hessian fly resistance but no specific biotype information is available. CI 14432 is a dark seeded tetraploid wheat with no known Hessian fly resistance. Florida 401, Florida 402, and GA-Wren's Abruzzi are diploid rye cultivars well adapted to the southeastern United States. Syn-T is a tetraploid rye population also well adapted to the southeastern United States.

Screening for Hessian fly resistance was conducted as described by Foster et al. (1988). Approximately 15 seeds of each line were planted in flats (7.0 x 37.5 x 55.0 cm) for each biotype screened in the initial screening. Twelve equidistant furrows in (1/3 sand, 1/3 peat, 1/3 top soil) potting mixture per flat were divided longitudinally to form 24

rows. Two central rows of each longitudinal section were seeded to combinations of standard susceptible and resistant differential common wheat cultivars having specific alleles for resistance to each Hessian fly biotype. When seedlings have reached the one to two leaf stage, approximately 200 adult Hessian flies flat⁻¹ were placed in tents. The adult flies were removed from the flats after 48 to 72 h. Approximately two weeks after oviposition, susceptible plants turn dark green and show distinctive dwarfing of the second and third leaves, caused by the feeding of the larvae. The number of susceptible and resistant plants was recorded 21 d after infestation.

Crosses among the various primary and secondary triticales (Table 1) had been made previously using C₃ generation plants; however, not all primary triticales had been crossed onto all secondary triticales in Table 1. Crosses were chosen for further investigation based on a preliminary screening of the parents involved in those crosses. These crosses involved primary triticales which were completely resistant to biotype E and secondary triticales which were completely susceptible to biotype E to minimize or eliminate confounding effects of genetic resistance other than that derived from CI 14908. Two hybrids were determined to meet this criterion: Florida 201/91PT579-G1 and MAH 13297-9/91PT579-G45. A third hybrid was included (Sunland/91PT579-G11) in which the primary triticales parent was completely resistant to biotype E of the Hessian fly but the secondary triticales parent, Sunland, had a low level of resistance in the initial screening. This cross was included because Sunland was the latest triticales variety released by the University of Florida. Sunland was released jointly between the University of Florida and the University of Georgia as a high yielding triticales adapted for the coastal plain region of the southeastern United States (Bruckner et al., 1992).

Table 1. Material used in initial screening to Hessian fly biotypes C, E, and L in 1993.

Material screened	Origin	Pedigree
CI 14908 (tetraploid wheat)	Ethiopia	Unknown
Florida 401 (rye)	Florida	1987 Released Population
FL8727-L1 (rye)	Florida	Improved seedling vigor selection of Florida 401
<u>Primary triticale</u>		
91PT579-G1	Florida	CI 14908/Florida 401
91PT579-G11	Florida	CI 14908/Florida 401
91PT579-G12	Florida	CI 14908/Florida 401
91PT579-G24	Florida	CI 14908/Florida 401
91PT579-G25	Florida	CI 14908/Florida 401
91PT579-G45	Florida	CI 14908/Florida 401
91PT579-G47	Florida	CI 14908/Florida 401
91PT579-G51	Florida	CI 14908/Florida 401
<u>Secondary triticale</u>		
Florida 201	Florida	Beagle/Maya II/Armadoillo 's'
Sunland	Georgia-Florida	Merino 's'/Juanillo
Lad 388	Poland	Unknown
CHD 1089	Poland	Unknown
Drago	Poland	Unknown
MAH 13297-9	Poland	Unknown
MAH 13524-1	Poland	Unknown
MAH 13524-4	Poland	Unknown
MAH 13534-9	Poland	Unknown
MAH 13534-12	Poland	Unknown
Trical T89-10	Resource Seeds Inc.	Unknown
<u>Common Wheat Differentials</u>		
Monon (H ₃) [†]		Unknown
Magnum (H ₅)		Unknown
Caldwell (H ₆)		Unknown
Seneca (H ₁ H ₃)		Unknown

[†]Hessian fly resistance allele contained.

Inadequate F_1 seed quantity for both generation advancement and Hessian fly screening from original crosses made it necessary to reconstitute the primary by secondary crosses of interest, using C_4 generation plants, in the winter of 1993-94. A portion of the F_1 seed obtained from these crosses was sent to Aberdeen, Idaho, along with F_2 seed from the original crosses for generation advancement in the summer of 1994.

Laboratory screening of parental lines, CI 14908, Florida 401, and the F_1 , F_2 , and F_3 populations for resistance to biotype E of the Hessian fly was conducted at the United States Department of Agriculture-Agriculture Research Service (USDA-ARS), Insect and Weed Control Research Unit, Purdue University, West Lafayette, Indiana, in the winter of 1994. Twenty five seed of the F_1 populations, and approximately 1000 seed of each F_2 and F_3 population were planted. Plants rated as resistant were returned to Quincy, Florida, and grown out in the greenhouse while those plants rated as susceptible were either killed by the Hessian fly or destroyed at Purdue.

An investigation of the tetraploid wheat CI 14908 was conducted to identify the Hessian fly resistance allele(s) which it contains. Several durum wheat lines were obtained from Dr. F. L. Patterson, Purdue University, West Lafayette, Indiana, and Dr. H. E. Bockelman, USDA-ARS, Aberdeen, Idaho, in which various Hessian fly resistance alleles were known to occur (Table 2).

Each of the tetraploid wheat lines in Table 2 were crossed onto CI 14908 in the greenhouse at Quincy, Florida, in the winter of 1993-94. F_1 seed were grown in Aberdeen, Idaho, for generation advancement in the summer of 1994. Remnant parental seed and F_2 populations were screened for resistance to biotype E of the Hessian fly at the

USDA-ARS, Insect and Weed Control Research Unit, Purdue University, West Lafayette, Indiana, in the winter of 1994. Plants rated as resistant were returned to Quincy, Florida, and grown out in the greenhouse while those plants rated as susceptible were either killed by the Hessian fly or destroyed at Purdue.

Table 2. Tetraploid wheat lines used in crossing with CI 14908 obtained from Drs. F. L. Patterson and H. E. Bockelman.

Germplasm line	Hessian fly resistance allele(s)
IN 8455	H ₉
IN 8458	H ₁₀
CI 17714, Elva	H ₉ , H ₁₀
IN 8456	H ₁₁
IN 8454	H ₁₂
IN 81601	H ₁₄
IN 81602	H ₁₅
PI 428435	H ₁₇
Iumillo	H ₁₈ [†]
PI 422297	H ₁₉ [†]
CI 17647	H ₁₄ , H ₁₅
CI 12080/PI 94587	H ₆ , H ₁₁ , H ₁₆
PI 355269, Jori	H ₂₀

[†]Plus symbol denotes at least one other unidentified resistance factor.

Cytogenetic Studies

Immature spikes for microspore analysis were collected in 1994 from the C₅ generation of the primary triticale lines (CI 14908/Florida 401) when the awn tips protruded approximately 1 to 2 cm from the boot (Table 3). Several samples were collected from each of the eight lines, fixed in Carnoy's solution (3 ethanol:1 acetic acid) for 24 h and stored in 70% ethanol (Darlington and La Coup, 1976) until meiotic chromosome analysis could be conducted. Diakinesis of prophase I, metaphase I and anaphase I chromosomes were stained with iron acetocarmine and counted using a Wild-M20 light microscope. Photomicrographs were made using Kodak TMAX ASA100 film. Percent aneuploidy was determined by dividing the number of meiotic cells with aberrant chromosome numbers by the total number of cells containing countable chromosomes including those cells with normal chromosome number. A minimum number of 42 cells in which chromosomes could be counted were examined in all primary triticale lines except 91PT579-G11 in which only two suitable samples could be collected and only 14 cells with countable chromosomes were observed.

Seed from 38 of the more than 600 primary triticale plants, grown in the greenhouse in 1992 at Quincy, Florida, were grown in the greenhouse in the summer of 1995 at Quincy, Florida, (Table 3). Of the plants grown in 1992, a subset of 70 had been threshed prior to my arrival at the University of Florida. A subset of 565, 1992 greenhouse primary triticale plants were threshed in 1995 and percent fertility was calculated by multiplying the number of spiklets plant⁻¹ by a factor of three, the most common number of fertile florets spiklet⁻¹ in secondary triticale.

Table 3. Primary triticale lines used for pollen stainability, fertility and cytological studies; grown in the greenhouse in the summer of 1995 at Quincy, Florida.

'95 entry number	Selection	Pedigree	Generation
1	91PT580-G5-G12	CI 14908/GA-Wren's Abruzzi	C ₄
2	91PT580-G32-G7	CI 14908/GA-Wren's Abruzzi	C ₄
3	91PT580-G24-G10	CI 14908/GA-Wren's Abruzzi	C ₄
4	91PT580-G1-G11	CI 14908/GA-Wren's Abruzzi	C ₄
5	91PT580-G21-G1	CI 14908/GA-Wren's Abruzzi	C ₄
6	91PT580-G5-G6	CI 14908/GA-Wren's Abruzzi	C ₄
7	91PT580-G27-G7	CI 14908/GA-Wren's Abruzzi	C ₄
8	91PT580-G8-G3	CI 14908/GA-Wren's Abruzzi	C ₄
9	91PT580-G21-G8	CI 14908/GA-Wren's Abruzzi	C ₄
10	91PT580-G24-G7	CI 14908/GA-Wren's Abruzzi	C ₄
11	91PT579-G37-G9	CI 14908/FL 401	C ₄
12	91PT579-G37-G8	CI 14908/FL 401	C ₄
13	91PT579-G37-G1	CI 14908/FL 401	C ₄
14	91PT579-G33-G13	CI 14908/FL 401	C ₄
15	91PT581-G1-G2	CI 14432/Syn-T (4X)	C ₄
16	91PT579-G37-G10	CI 14908/FL 401	C ₄
17	91PT579-G46-G6	CI 14908/FL 401	C ₄
18	91PT579-G18-G4	CI 14908/FL 401	C ₄
19	91PT579-G28-G3	CI 14908/FL 401	C ₄
20	91PT579-G13-G9	CI 14908/FL 401	C ₄
21	91PT575-G3-G13	Swan 's'/FL 402	C ₄
22	91PT575-G1-G2	Swan 's'/FL 402	C ₄
23	91PT575-G1-G8	Swan 's'/FL 402	C ₄
24	91PT575-G2-G3	Swan 's'/FL 402	C ₄
25	91PT575-G3-G10	Swan 's'/FL 402	C ₄
26	91PT575-G3-G6	Swan 's'/FL 402	C ₄

Table 3--continued.

'95 entry number	Selection	Pedigree	Generation
27	91PT575-G3-G4	Swan 's'/FL 402	C ₄
28	91PT575-G2-G6	Swan 's'/FL 402	C ₄
29	91PT575-G1-G4	Swan 's'/FL 402	C ₄
30	91PT575-G4-G10	Swan 's'/FL 402	C ₄
31	91PT579-G1-PGE4	CI 14908/FL 401	C ₅
32	91PT579-G11-PGE11	CI 14908/FL 401	C ₅
33	91PT579-G24-PGE24	CI 14908/FL 401	C ₅
34	91PT579-G32-PGE2	CI 14908/FL 401	C ₅
35	91PT579-G32-PGE1	CI 14908/FL 401	C ₅
36	91PT579-G41-PGE3	CI 14908/FL 401	C ₅
37	91PT579-G45-PGE18	CI 14908/FL 401	C ₅
38	91PT579-G47-PGE16	CI 14908/FL 401	C ₅

Entries 1-10 (CI 14908/GA Wren's Abruzzi) were progeny of those plants with the highest percent fertility of the 565 plants in which percent fertility had been calculated. Entries 11-20 were progeny from those lines with the highest percent fertility with a pedigree different from CI 14908/GA Wren's Abruzzi (Table 3). Entries 21-30 (Swan 's/Florida 402) were chosen from the subset of 70 plants which had been previously threshed, each had more than 100 seed available. Entries 31-38 had the highest percent fertility primary triticales plants (CI 14908/Florida 401) which were screened for resistance to biotype E of the Hessian fly in 1995. Entries 1-30 were C₄ generation plants, while entries 31-38 were C₅ generation plants.

Twelve seeds line⁻¹ were planted in speedling flats. Replanting of seeds which did not germinate was performed as needed. Root tips were collected from six plants line⁻¹, except 91PT579-G18-G4 of which only four plants germinated. Plants from which root tips were collected were transplanted into 15 cm pots and grown to maturity in an air-conditioned greenhouse during the summer of 1995 at Quincy, Florida. Root tips were pretreated in ice water for 24 h, transferred to Carnoy's solution and fixed for 12 h, and subsequently transferred to 70% ethanol until mitotic chromosome counts could be conducted. Root tips were stained with iron acetocarmine and counts were determined at 200X, 400X, or 500X magnification, depending on squash clarity, on a Leitz Wetzler-Dialux light microscope.

Immature spikes for microspore analysis were collected from each plant when awn tips extruded from the boot approximately 3 to 6 mm. Spikes were fixed in Carnoy's solution for 24 h before transferring to 70% ethanol for storage. All remaining spikes on

the plants were covered with a bag made of 40 mm dialysis tubing immediately upon emergence from the boot to ensure self-pollination. Pollen was collected from a single spike at anthesis from each plant. A small amount of pollen was collected on a glass microscope slide. A drop of iron acetocarmine stain was added to the microscope slide and all pollen grains contained within the drop were scored as stained or unstained (completely clear). To minimize sampling error, all pollen grains within the drop of stain were scored. Empty pollen grains have a tendency to float to the edges of a low viscosity fluid (Radford et al., 1974). Other pollen staining procedures have been used by other researchers to predict pollen viability; however, most are more time consuming than the iron acetocarmine technique and not necessarily more reliable predictors of viability (Joppa et al., 1968; Radford et al., 1974). Chi square tests of independence, using an R x C table (Snedecor and Cochran, 1967), were conducted for pollen stainability and seed set to test for homogeneity within each of the 38 entries in Table 3.

Hessian Fly Screening for Germplasm Identification

Approximately 15 plants entry¹ obtained from 91 plants grown in the greenhouse at Quincy, Florida, were screened for resistance to Hessian fly biotype L at Purdue University (Table 4). Entries 1-10 were selected from plants grown in the summer of 1995. Entries 1-9 were identified as having a combination of relatively high fertility and pollen stainability as well as having plump, unshriveled seed. Entry 10 was included in this study based primarily on its pedigree (CI 14908/ Florida 401). Entry 10 had the highest percent fertility and least shriveled seed of those plants with the pedigree

CI 14908/Florida 401 grown in the greenhouse in 1995. Entries 11-91 (Table 4) were a subset of the progeny from the best (producing a large quantity of high quality seed) individual plants of the Hessian fly biotype E resistant F_2 and F_3 populations returned from Purdue University and grown to maturity in the greenhouse at Quincy, Florida, in the winter of 1994-1995. These plants may have been either heterozygous or homozygous resistant to Hessian fly biotype E.

Table 4. Triticale screened to Hessian fly biotype L at Purdue University in 1996.

Entry number	Selection	Pedigree	Generation
1	91PT580-G24-G10-G4(6)	CI 14908/GA-Wren's Abruzzi	C ₅
2	91PT575-G1-G2-G22(1)	Swan s'/FL 402	C ₅
3	91PT575-G1-G8-G23(5)	Swan s'/FL 402	C ₅
4	91PT575-G2-G3-G24(1)	Swan s'/FL 402	C ₅
5	91PT575-G3-G10-G25(3)	Swan s'/FL 402	C ₅
6	91PT575-G3-G4-G27(2)	Swan s'/FL 402	C ₅
7	91PT575-G1-G4-G29(1)	Swan s'/FL 402	C ₅
8	91PT575-G1-G4-G29(6)	Swan s'/FL 402	C ₅
9	91PT575-G4-G10-G30(6)	Swan s'/FL 402	C ₅
10	91PT579-G32-PGE1-G35(5)	CI 14908/FL 401	C ₆
11	(FL201/91PT579-G1)-PGE1-G21	FL201/91PT579-G1	F ₃
12	(FL201/91PT579-G1)-PGE1-G22	FL201/91PT579-G1	F ₃
13	(FL201/91PT579-G1)-PGE1-G24	FL201/91PT579-G1	F ₃
14	(FL201/91PT579-G1)-PGE1-G33	FL201/91PT579-G1	F ₃
15	(FL201/91PT579-G1)-PGE1-G40	FL201/91PT579-G1	F ₃
16	(FL201/91PT579-G1)-PGE1-G42	FL201/91PT579-G1	F ₃
17	(FL201/91PT579-G1)-PGE1-G43	FL201/91PT579-G1	F ₃

Table 4--continued.

Entry number	Selection	Pedigree	Generation
18	(FL201/91PT579-G1)-PGE1-G54	FL201/91PT579-G1	F ₃
19	(FL201/91PT579-G1)-PGE1-G55	FL201/91PT579-G1	F ₃
20	(FL201/91PT579-G1)-PGE1-G61	FL201/91PT579-G1	F ₃
21	(FL201/91PT579-G1)-PGE1-G62	FL201/91PT579-G1	F ₃
22	(FL201/91PT579-G1)-PGE1-G70	FL201/91PT579-G1	F ₃
23	(FL201/91PT579-G1)-PGE1-G72	FL201/91PT579-G1	F ₃
24	(FL201/91PT579-G1)-PGE1-G73	FL201/91PT579-G1	F ₃
25	(Sunland/91PT579-G11)-PGE2-G9	Sunland/91PT579-G11	F ₃
26	(Sunland/91PT579-G11)-PGE2-G14	Sunland/91PT579-G11	F ₃
27	(Sunland/91PT579-G11)-PGE2-G21	Sunland/91PT579-G11	F ₃
28	(Sunland/91PT579-G11)-PGE2-G46	Sunland/91PT579-G11	F ₃
29	(Sunland/91PT579-G11)-PGE2-G50	Sunland/91PT579-G11	F ₃
30	(Sunland/91PT579-G11)-PGE2-G51	Sunland/91PT579-G11	F ₃
31	(Sunland/91PT579-G11)-PGE2-G53	Sunland/91PT579-G11	F ₃
32	(Sunland/91PT579-G11)-PGE2-G56	Sunland/91PT579-G11	F ₃
33	(Sunland/91PT579-G11)-PGE2-G59	Sunland/91PT579-G11	F ₃
34	(Sunland/91PT579-G11)-PGE2-G60	Sunland/91PT579-G11	F ₃

Table 4--continued.

Entry number	Selection	Pedigree	Generation
35	(Sunland/91PT579-G11)-PGE2-G65	Sunland/91PT579-G11	F ₃
36	(Sunland/91PT579-G11)-PGE2-G74	Sunland/91PT579-G11	F ₃
37	(Sunland/91PT579-G11)-PGE2-G75	Sunland/91PT579-G11	F ₃
38	(Sunland/91PT579-G11)-PGE2-G78	Sunland/91PT579-G11	F ₃
39	(MAH13297-9/91PT579-G45)-PGE3-G5	MAH13297-9/91PT579-G45	F ₃
40	(MAH13297-9/91PT579-G45)-PGE3-G6	MAH13297-9/91PT579-G45	F ₃
41	(MAH13297-9/91PT579-G45)-PGE3-G8	MAH13297-9/91PT579-G45	F ₃
42	(MAH13297-9/91PT579-G45)-PGE3-G9	MAH13297-9/91PT579-G45	F ₃
43	(MAH13297-9/91PT579-G45)-PGE3-G10	MAH13297-9/91PT579-G45	F ₃
44	(MAH13297-9/91PT579-G45)-PGE3-G12	MAH13297-9/91PT579-G45	F ₃
45	(MAH13297-9/91PT579-G45)-PGE3-G13	MAH13297-9/91PT579-G45	F ₃
46	(MAH13297-9/91PT579-G45)-PGE3-G15	MAH13297-9/91PT579-G45	F ₃
47	(MAH13297-9/91PT579-G45)-PGE3-G18	MAH13297-9/91PT579-G45	F ₃
48	(MAH13297-9/91PT579-G45)-PGE3-G19	MAH13297-9/91PT579-G45	F ₃
49	(MAH13297-9/91PT579-G45)-PGE3-G20	MAH13297-9/91PT579-G45	F ₃
50	(MAH13297-9/91PT579-G45)-PGE3-G21	MAH13297-9/91PT579-G45	F ₃
51	(MAH13297-9/91PT579-G45)-PGE3-G22	MAH13297-9/91PT579-G45	F ₃

Table 4—continued.

Entry number	Selection	Pedigree	Generation
52	(MAH13297-9/9IPT579-G45)-PGE3-G23	MAH13297-9/9IPT579-G45	F ₃
53	(MAH13297-9/9IPT579-G45)-PGE3-G25	MAH13297-9/9IPT579-G45	F ₃
54	(FL201/9IPT579-G1)-PGE4-G1	FL201/9IPT579-G1	F ₄
55	(FL201/9IPT579-G1)-PGE4-G2	FL201/9IPT579-G1	F ₄
56	(FL201/9IPT579-G1)-PGE4-G4	FL201/9IPT579-G1	F ₄
57	(Sunland/9IPT579-G11)-PGE5-G1	Sunland/9IPT579-G11	F ₄
58	(Sunland/9IPT579-G11)-PGE5-G4	Sunland/9IPT579-G11	F ₄
59	(Sunland/9IPT579-G11)-PGE5-G5	Sunland/9IPT579-G11	F ₄
60	(Sunland/9IPT579-G11)-PGE5-G6	Sunland/9IPT579-G11	F ₄
61	(Sunland/9IPT579-G11)-PGE5-G7	Sunland/9IPT579-G11	F ₄
62	(Sunland/9IPT579-G11)-PGE5-G10	Sunland/9IPT579-G11	F ₄
63	(Sunland/9IPT579-G11)-PGE5-G11	Sunland/9IPT579-G11	F ₄
64	(Sunland/9IPT579-G11)-PGE5-G12	Sunland/9IPT579-G11	F ₄
65	(Sunland/9IPT579-G11)-PGE5-G15	Sunland/9IPT579-G11	F ₄
66	(Sunland/9IPT579-G11)-PGE5-G16	Sunland/9IPT579-G11	F ₄
67	(Sunland/9IPT579-G11)-PGE5-G18	Sunland/9IPT579-G11	F ₄
68	(Sunland/9IPT579-G11)-PGE5-G22	Sunland/9IPT579-G11	F ₄

Table 4--continued

Entrv number	Selection	Pedigree	Generation
69	(Sunland/9 PTS79-G11)-PGE5-G23	Sunland/9 PTS79-G11	F ₄
70	(Sunland/9 PTS79-G11)-PGE5-G25	Sunland/9 PTS79-G11	F ₄
71	(MAH13297-9/9 PTS79-G45)-PGE6-G1	MAH13297-9/9 PTS79-G45	F ₄
72	(MAH13297-9/9 PTS79-G45)-PGE6-G2	MAH13297-9/9 PTS79-G45	F ₄
73	(MAH13297-9/9 PTS79-G45)-PGE6-G3	MAH13297-9/9 PTS79-G45	F ₄
74	(MAH13297-9/9 PTS79-G45)-PGE6-G4	MAH13297-9/9 PTS79-G45	F ₄
75	(MAH13297-9/9 PTS79-G45)-PGE6-G8	MAH13297-9/9 PTS79-G45	F ₄
76	(MAH13297-9/9 PTS79-G45)-PGE6-G9	MAH13297-9/9 PTS79-G45	F ₄
77	(MAH13297-9/9 PTS79-G45)-PGE6-G10	MAH13297-9/9 PTS79-G45	F ₄
78	(MAH13297-9/9 PTS79-G45)-PGE6-G11	MAH13297-9/9 PTS79-G45	F ₄
79	(MAH13297-9/9 PTS79-G45)-PGE6-G12	MAH13297-9/9 PTS79-G45	F ₄
80	(MAH13297-9/9 PTS79-G45)-PGE6-G14	MAH13297-9/9 PTS79-G45	F ₄
81	(MAH13297-9/9 PTS79-G45)-PGE6-G17	MAH13297-9/9 PTS79-G45	F ₄
82	(MAH13297-9/9 PTS79-G45)-PGE6-G19	MAH13297-9/9 PTS79-G45	F ₄
83	(MAH13297-9/9 PTS79-G45)-PGE6-G20	MAH13297-9/9 PTS79-G45	F ₄
84	(MAH13297-9/9 PTS79-G45)-PGE6-G21	MAH13297-9/9 PTS79-G45	F ₄
85	(MAH13297-9/9 PTS79-G45)-PGE6-G24	MAH13297-9/9 PTS79-G45	F ₄

Table 4--continued

Entry number	Selection	Pedigree	Generation
86	(MAH13297-9/9 PT579-G45)-PGE6-G28	MAH13297-9/9 PT579-G45	F ₄
87	(MAH13297-9/9 PT579-G45)-PGE6-G30	MAH13297-9/9 PT579-G45	F ₄
88	(MAH13297-9/9 PT579-G45)-PGE6-G31	MAH13297-9/9 PT579-G45	F ₄
89	(MAH13297-9/9 PT579-G45)-PGE6-G33	MAH13297-9/9 PT579-G45	F ₄
90	(MAH13297-9/9 PT579-G45)-PGE6-G35	MAH13297-9/9 PT579-G45	F ₄
91	(MAH13297-9/9 PT579-G45)-PGE6-G36	MAH13297-9/9 PT579-G45	F ₄

RESULTS AND DISCUSSION

Triticale Classical Genetic Studies

Initial screening for resistance to Hessian fly biotypes C, E, and L of eight C₄ (third self-pollinated generation after colchicine doubling) primary triticales, eleven secondary triticales, CI 14908 tetraploid wheat, Florida 401 and FL8727-L1 rye, and the four standard common wheat differentials (Monon, Magnum, Caldwell, and Seneca) were conducted in 1993 (Table 5). In theory, doubled haploid plants should be homozygous at all loci. None of the primary triticales lines tested were uniformly resistant to all three of the biotypes tested but each of the primary triticales lines except 91PT579-G47, and 91PT579-G51 were uniformly resistant to at least one biotype. Neither were any of the primary triticales lines uniformly resistant to both Hessian fly biotypes E and L as was CI 14908, the tetraploid wheat parent of 91PT579. Primary triticales lines 91PT579-G1, 91PT579-G11, 91PT579-G12, and 91PT579-G45 were uniformly resistant to biotype E of the Hessian fly in the C₄ generation. The uniform biotype E resistance of these primary lines, coupled with uniform susceptibility to biotype E of secondary triticales which had been previously crossed with these primary lines (except 91PT579-G12), was the reason for their use in subsequent studies. High levels of biotype E resistance were also observed in 91PT579-G24 and 91PT579-G47 although the resistance was not uniform as expected. Three of these primary triticales lines had a combination of high levels of biotype C and

Table 5. Seedling response to Hessian fly biotypes C, E, and L of primary and secondary triticales, CI 14908 tetraploid wheat, Florida 401, and FL8727-L1 rye in 1993.

Population	Biotype					
	C		E		L	
	R [†]	S [†]	R	S	R	S
CI 14908	5	2	2	0	6	0
Florida 401	0	11	0	9	0	10
FL8727-L1	0	13	0	10	0	14
<u>Primary triticale</u>						
91PT579-G1	5	3	5	0	3	5
91PT579-G11	7	5	10	0	3	9
91PT579-G12	7	6	12	0	6	7
91PT579-G24	13	0	11	2	2	8
91PT579-G25	8	4	7	7	8	0
91PT579-G45	12	0	12	0	2	9
91PT579-G47	12	4	11	1	4	10
91PT579-G51	9	2	7	4	4	6
<u>Secondary triticale</u>						
Florida 201	13	0	0	10	13	1
Sunland	15	0	2	7	10	1
Lad 388	0	9	0	8	0	12
CHD 1089	0	7	8	2	0	12
Drago	0	6	0	5	0	7
MAH 13297-9	13	0	0	12	10	0
MAH 13524-1	17	0	0	11	9	5
MAH 13524-4	12	0	0	12	10	2
MAH 13534-9	11	1	0	12	8	2
MAH 13534-12	13	0	0	9	6	3
Trical T89-10	2	0	5	0	10	0
<u>Differentials</u>						
Monon (H ₃) [‡]	12	0	0	13	0	12
Magnum (H ₃)	21	0	22	0	0	23
Caldwell (H ₆)	0	14	13	0	0	15
Seneca (H ₁ H ₆)	0	25	11	0	0	6

[†]R=number of resistant plants, S=number of susceptible plants.

[‡]Hessian fly resistance allele involved.

biotype E resistance (91PT579-G24, 91PT579-G45, 91PT579-G47), but the only primary triticale that was observed as being highly resistant to Hessian fly biotype L was 91PT579-G25 .

Secondary triticale cultivars and lines expressed a much higher level of Hessian fly resistance than was expected (Table 5), although only two were resistant to biotype E. Florida 201 was not known to have any Hessian fly resistance and Sunland triticale was only known to carry resistance to biotype D (Bruckner et al., 1992). Hessian fly biotype D has not been observed in Northwest Florida in recent years. Buntin and Raymer (1989b) reported Florida 201 and Sunland triticale as being susceptible to Hessian fly populations found in Georgia. Lad 388 and Drago, two of the eight lines originating from Poland, were completely susceptible to Hessian fly biotypes C, E and L. CHD 1089 was the only Polish line that carried resistance to biotype E. The five Polish lines (MAH in pedigree designation) had high levels of resistance to biotypes C and L, although the resistance to biotype L was more variable in all MAH lines except MAH 13279-9. Trical T89-10 appeared to be completely resistant to biotypes C, E and L. The combination of Hessian fly biotype L resistance in the absence of biotype E resistance has not been reported previously. All Hessian fly resistance alleles previously reported to confer resistance to biotype L, also conferred resistance to biotype E.

Since 91PT579-G1 and 91PT579-G11 were uniformly resistant to biotype E of the Hessian fly in the C₄ generation, there was no reason to predict they would segregate for resistance in the C₅ generation, as was the case (Table 6). Many theories explaining the unexpected segregation patterns can be proposed. Natural outcrossing with a susceptible

Table 6. C₃ generation primary, secondary triticale lines, secondary triticale populations and wheat differentials screened for resistance to biotype E of the Hessian fly in 1994.

	C ₃ generation		F ₂				F ₃			
	Primary Triticale	R-S [†]	Observed R-S	Expected [‡] R-S	χ ²	Expected R-S	Observed R-S	χ ²	Expected R-S	χ ²
Primary Triticale										
	91PT579-G1	11-8								
	91PT579-G11	12-11								
	91PT579-G45	24-0								
Secondary triticale										
	Florida 201	0-17								
	Sunland	0-28								
	MAH 13297-9	3-26								
Population										
	Florida 201/91PT579-G1	9-12	21-0	296-481	**	583-194	58-187	**	154-91	**
	Sunland/91PT579-G11	12-1	13-0	442-418	**	645-215	237-362	**	377-222	**
	MAH 13297-9/91PT579-G45	19-1	20-0	410-309	**	540-180	360-433	**	500-293	**
Differentials										
	Monon (H ₃) [‡]	S								
	Magnum (H ₃)	R								
	Caldwell (H ₆)	R								
	Seneca (H ₄ H ₆)	R								

[†]R= resistant plant number, S=susceptible plant number.

[‡]Hessian fly resistance allele involved.

[§]One locus, two allele model with complete dominance assumed.

** Indicates significant difference between observed and expected values at $P=0.01$ level.

line may have taken place in the greenhouse in the C_4 generation. However, the expected segregation ratios of resistant to susceptible from such an outcross would not be expected to be so low; nearly 1:1. A much higher level of resistance would be expected because only seed from those florets that outcrossed would be expected to segregate, and then only at a 3:1 resistant to susceptible ratio if a single locus, two-allele model with complete dominance is assumed. Complete or partial dominance gene action is the most common gene action of previously identified Hessian fly resistance loci (Patterson et al., 1992). Outcrossing may also have occurred in a generation earlier than the C_4 but not detected in initial screening of the primary triticales lines due to inadequate sample size.

The unexpected susceptibility within the primary triticales lines might have occurred because of high levels of aneuploidy. A deletion of the chromosomes that contain the Hessian fly resistance locus(i) contributed by CI 14908 would lead to susceptibility to Hessian fly. Non-random chromosome deletions may occur while still producing viable offspring. Aneuploidy also leads to partial sterility and makes florets more susceptible to outcrossing by opening and exposing stigmas to any foreign pollen source.

Additionally, primary and secondary triticales seedlings can be lacking in vigor even when the full complement of chromosomes is present. Therefore, some of those seedlings may have been incorrectly classified as susceptible. And lastly, there is a possibility that the biotype E population of the Hessian fly used had been contaminated with other biotypes. This is the least probable explanation because wheat lines used as differentials reacted as expected. It is likely that some combination of these factors led to the unexpected levels of susceptibility to the Hessian fly in 91PT579-G1 and 91PT579-G11.

Secondary triticale lines which were used in primary by secondary crosses were also screened for resistance to biotype E of the Hessian fly in both 1993 and 1994 (Table 6). Low levels of biotype E resistance detected in 'Sunland' in 1993 were no longer apparent in the 1994 screening results. Low levels of biotype E resistance in MAH 13297-9 appeared in 1994 that were not detected in the 1993 screening. The only secondary triticale which remained uniformly susceptible to biotype E in both 1993 and 1994 was Florida 201 .

The variability in resistance levels in these secondary triticale lines was disturbing. Not detecting resistance in MAH 13297-9 may have been caused by inadequate sampling but the disappearance of resistance in Sunland in 1994 suggests that differing seed lots of these lines may be quite genetically different with respect to Hessian fly resistance. Higher levels of natural outcrossing than previously predicted may be the cause.

Three generations (F_1 , F_2 , and F_3) of primary by secondary bulk populations were screened for resistance to biotype E of the Hessian fly in 1994 (Table 6). F_1 populations were predicted to be completely resistant to biotype E of the Hessian fly assuming that the primary triticale lines used in the development of the hybrids were homozygous dominant for resistance genes derived from CI 14908. The Florida 201/91PT579-G1 hybrid segregated at a ratio of 3:4 resistant to susceptible. This unexpected segregation was similar to segregation observed in 91PT579-G1 in the 1994 screening. A single susceptible reaction was also observed in each of the other two hybrids screened.

The susceptible F_1 plants in both Sunland/91PT579-G11 and MAH 13297-9/91PT579-G45 could possibly be explained by inaccurate classification of weak plants. Much higher levels of susceptibility than would be expected from a single locus two-allele model expressing complete dominance were observed in both the F_2 and F_3 populations. F_2 populations were derived directly from the hybrid populations in Table 6 (C_4 primary triticale lines) while F_3 populations were derived from crosses made with C_3 primary triticale lines. The most logical explanation for the higher than expected levels of susceptibility is natural outcrossing. Male sterility, associated with aneuploidy, tends to open florets, exposing stigmas to foreign pollen.

Durum Allelic Screening Study

Three tetraploid wheat lines, PI 355269, IN 81601, and PI 422297 were susceptible to biotype E of the Hessian fly in a seedling screening test conducted in 1994 (Table 7). These lines contained Hessian fly resistance alleles H_{20} , H_{14} , and H_{19}^+ , respectively. While this does not exclude the possibility that CI 14908 contains these dominant alleles, at least these loci are not responsible for the resistance to biotype E of the Hessian fly that is observed in CI 14908. High levels of resistance were observed in lines containing H_6 , H_9 , H_{10} , H_{11} , H_{12} , H_{15} , H_{16} , H_{17} , and H_{18}^+ . While IN 80164 (H_{16}) was screened for resistance to biotype E of the Hessian fly, it was not involved in crosses with CI 14908.

Table 7. Seedling reaction of CI 14908 and tetraploid wheats used in crosses with CI 14908 to biotype E of the Hessian fly in 1994.

Tetraploid wheat	Hessian fly resistance allele(s)	Reaction R-S [†]
CI 14908	unknown	25-0
CI 17647	H ₁₄ , H ₁₅	27-0
PI 428435	H ₁₇	27-1
PI 355296, Jori	H ₂₀	2-26
CI 17714, Elva	H ₉ , H ₁₀	26-0
CI 12080	H ₆ , H ₁₁ , H ₁₆	29-0
IN 8455	H ₉	21-0
IN 8458	H ₁₀	28-0
IN 8456	H ₁₁	23-0
IN 8454	H ₁₂	12-2
IN 81601	H ₁₄	2-18
IN 81602	H ₁₅	20-0
Iumillo	H ₁₈ [‡]	22-0
PI 422297	H ₁₉ [‡]	2-20
IN 80164	H ₁₆	20-0

[†]R= resistant plant number, S=susceptible plant number.

[‡]Plus symbol denotes at least one unidentified Hessian fly resistance factor.

Screening of F_2 durum populations to biotype E of the Hessian fly was conducted in 1994 (Table 8). Six populations were completely resistant to the Hessian fly while the remaining seven populations were segregating for resistance. Susceptible progeny were observed in F_2 populations when CI 14908 was involved in crosses containing H_{10} , H_{11} , H_{12} , H_{14} , H_{17} , H_{19}^+ , and H_{20} in the absence of other Hessian fly resistance alleles. If CI 14908 carried common alleles conferring resistance to Hessian fly biotype E at these loci, no segregation would be expected. CI 14908 may carry any combination of

Table 8. Seedling reaction of F_2 tetraploid wheat populations containing known and unknown Hessian fly resistance alleles screened to biotype E of the Hessian fly in 1994.

Pedigree	Hessian fly resistance allele(s) from ♀ parent	R-S [†]
CI 17647/CI 14908	H_{14} , H_{15}	130-0
PI 428435/CI 14908	H_{17}	171-5
PI 355269/CI 14908	H_{20}	138-6
CI 17714/CI 14908	H_9 , H_{10}	166-0
CI 12080/CI 14908	H_6 , H_{11} , H_{16}	183-0
IN 8455/CI 14908	H_9	182-0
IN 8458/CI 14908	H_{10}	137-33
IN8456/CI 14908	H_{11}	149-50
IN 8454/CI 14908	H_{12}	150-54
IN 81601/CI 14908	H_{14}	139-51
IN 81602/CI 14908	H_{15}	161-0
Iumillo/CI 14908	$H_{18}^{+‡}$	174-0
PI 422297/CI 14908	$H_{19}^{+‡}$	158-8

[†]R= resistant plant number, S=susceptible plant number.

[‡]Plus symbol denotes at least one other unidentified Hessian fly resistance factor.

common alleles at H_6 , H_9 , H_{15} , H_{16} , and/or H_{18}^+ since no segregation was observed in crosses involving these loci and may carry resistance factors at one or more previously undescribed loci.

Cytological Studies

Only CI 14908, four C_4 and two C_5 primary triticales derived from (CI 14908 /Florida 401) were uniformly resistant when screened to Hessian fly biotype E (Table 9). Primary triticales 91PT579-G45 was the only triticales line completely resistant to biotype E in both C_4 and C_5 generations, however, only one plant of 91PT579-G47 was classified as susceptible in the C_4 generation and was completely resistant in the C_5 generation. Other C_5 lines were either segregating or were uniformly susceptible to Hessian fly biotype E. Based on the seedling screening tests of C_4 and C_5 lines, only two lines (91PT579-G45 and 91PT579-G47) show adequate resistance to Hessian fly biotype E to meet the objectives of this research.

Although 91PT579-G45 was completely resistant in both the C_4 and C_5 generations, 23% of the C_5 microspores had some degree of aneuploidy (Table 9). Primary triticales 91PT579-G47 and 91PT579-G51 were more stable with only 5% C_5 microspores containing aneuploid cells (Fig. 1) but 91PT579-G51 was completely susceptible to biotype E in the C_5 generation. Primary triticales 91PT579-G25 was also uniformly susceptible but 44% of the microspores showed some degree of aneuploidy. No apparent relationship between aneuploidy in the eight primary triticales lines and segregation for Hessian fly resistance was observed.

Table 9. Seedling reaction to Hessian fly biotype E for eight C₄ and C₅ primary triticales lines (CI 14908/Florida 401), CI 14908 tetraploid wheat, and Florida 401 rye and percent developing microspores with unpaired univalents at diakinesis in C₅ generation primary triticales lines.

Line	C ₄			C ₅		
	R [†]	S [†]		R	S	Cells with Aneuploidy (%)
CI 14908	2	0		25	0	—
Florida 401	0	9		0	25	—
<u>Primary triticales</u>						
91PT579-G1	5	0		11	8	17
91PT579-G11	10	0		12	11	29
91PT579-G12	12	0		2	2	57
91PT579-G24	11	2		14	4	64
91PT579-G25	7	7		0	12	44
91PT579-G45	12	0		24	0	23
91PT579-G47	11	1		21	0	5
91PT579-G51	7	4		0	23	5

†R=Number of resistant plants, S=Number of susceptible plants



Fig. 1. Photomicrograph of PT579-G45 at diakinesis showing 20 ring bivalent pairs and 2 univalents (▲), 250X magnification.

Additional cytological studies were conducted in 1995 on 38 primary triticales lines which were originally grown in the greenhouse at Quincy, Florida, in 1992. Mitotic and meiotic chromosomes counts revealed that 87% of the plants within these 38 triticales lines contained a full chromosome complement. Approximately 2% of the plants contained fewer chromosomes than expected based on pedigree while the remaining 11% of the plants could not be characterized. Three of the six plants in entry 15 (CI 14432/Syn-T) contained the full complement of 56 chromosomes (Fig. 2) that was expected from this AABBRRRR line [allotetraploid wheat (AABB) X autotetraploid rye (RRRR) cross], while the other three plants from entry 15 appeared to contain 42 chromosomes. Plant 4



Fig. 2. Photomicrograph of a root tip cell of primary triticale (CI 14432/Syn-T)
 $2n=8x=56$, 250X magnification.

of entry 14 contained only 34 chromosomes, confirmed by both mitotic and meiotic counts, and one plant of entry 31 only had 27 mitotic chromosomes, although this could not be confirmed with meiotic analysis because no anthers ever developed on the spikes. These were the only two plants that could be characterized as having an incomplete genomic chromosome number. Because most of the plants contained a complete set of 42 somatic chromosomes, the hypothesis that non-random chromosome loss as a cause of high levels of Hessian fly susceptibility is unlikely.

The mean seed set of plants grown in the greenhouse in 1995 at Quincy, Florida, tended to be lower than the percent seed set from the 1992 greenhouse plants from which they were derived (Table 10). This is possibly a result of different greenhouse

Table 10. Primary triticate lines used for pollen stainability, fertility and cytological studies; grown in the greenhouse in the summer of 1995 at Quincy, Florida.

1995 greenhouse entry number	1992 Greenhouse				1995 Greenhouse			
	Selection	Generation	Spiklet no.	Seed no.	Percent seed set	Generation	Mean percent pollen stained	Mean percent seed set
1	91PT580-G5-G12	C ₄	65	112	57.4	C ₅	89.7	26.8
2	91PT580-G32-G7	C ₄	69	118	57.0	C ₅	91.2	32.1
3	91PT580-G24-G10	C ₄	31	51	54.8	C ₅	85.2	42.8
4	91PT580-G1-G11	C ₄	53	87	54.7	C ₅	88.2	68.3
5	91PT580-G21-G1	C ₄	39	63	53.8	C ₅	85.5	19.8
6	91PT580-G5-G6	C ₄	44	71	53.8	C ₅	87.0	24.3
7	91PT580-G27-G7	C ₄	41	66	53.7	C ₅	87.8	22.5
8	91PT580-G8-G3	C ₄	45	72	53.3	C ₅	84.8	15.5
9	91PT580-G21-G8	C ₄	38	60	52.6	C ₅	82.0	19.5
10	91PT580-G24-G7	C ₄	44	69	52.3	C ₅	75.3	13.7
11	91PT579-G37-G9	C ₄	61	85	46.4	C ₅	88.8	43.2
12	91PT579-G37-G8	C ₄	46	64	46.4	C ₅	48.8	32.5
13	91PT579-G37-G1	C ₄	44	52	39.4	C ₅	65.7	45.3
14	91PT579-G33-G13	C ₄	64	75	39.1	C ₅	45.7	22.0
15	91PT581-G1-G2	C ₄	72	84	38.9	C ₅	85.5	50.7
16	91PT579-G37-G10	C ₄	48	55	38.2	C ₅	72.3	51.8
								3

Table 10—continued

1995 greenhouse entry number	1992 Greenhouse				1995 Greenhouse			
	Selection	Generation	Spiklet no.	Seed no.	Percent seed set	Generation	Mean percent pollen stained	Mean percent seed set
17	91PT579-G46-G6	C ₄	56	62	36.9	C ₅	32.8	30.2
18	91PT579-G18-G4	C ₄	26	28	35.9	C ₅	7.5	32.1
19	91PT579-G28-G3	C ₄	31	33	35.5	C ₅	24.3	25.5
20	91PT579-G13-G9	C ₄	48	50	34.7	C ₅	17.7	27.3
21	91PT575-G3-G13	C ₄	?	166		C ₅	87.0	72.5
22	91PT575-G1-G2	C ₄	?	153		C ₅	69.8	78.3
23	91PT575-G1-G8	C ₄	?	149		C ₅	72.2	71.8
24	91PT575-G2-G3	C ₄	?	134		C ₅	86.8	85.7
25	91PT575-G3-G10	C ₄	?	131		C ₅	67.0	62.3
26	91PT575-G3-G6	C ₄	?	126		C ₅	69.0	61.0
27	91PT575-G3-G4	C ₄	?	125		C ₅	87.8	78.7
28	91PT575-G2-G6	C ₄	?	121		C ₅	64.8	26.2
29	91PT575-G1-G4	C ₄	?	118		C ₅	78.2	91.7
30	91PT575-G4-G10	C ₄	?	114		C ₅	66.5	69.2
31	91PT579-G1-PGE4	C ₅	56	79	47.0	C ₆	46.3	23.8
32	91PT579-G11-PGE11	C ₅	79	108	45.6	C ₆	54.8	24.3

Table 10--continued

1995 greenhouse entry number	1992 Greenhouse					1995 Greenhouse		
	Selection	Generation	Spiklet no.	Seed no.	Percent seed set	Generation	Mean percent pollen stained	Mean percent seed set
33	91PT579-G24-PGE24	C ₅	61	81	44.3	C ₆	84.7	50.1
34	91PT579-G32-PGE2	C ₅	56	137	81.5	C ₆	89.3	43.0
35	91PT579-G32-PGE1	C ₅	78	118	50.4	C ₆	71.8	52.3
36	91PT579-G41-PGE3	C ₅	91	110	40.3	C ₆	72.8	10.8
37	91PT579-G45-PGE18	C ₅	31	40	43.0	C ₆	87.3	45.7
38	91PT579-G47-PGE16	C ₅	63	83	43.9	C ₆	76.0	39.7

management practices. All spikes were covered with dialysis tubing, to ensure self-pollination, in 1995, whereas spikes were left uncovered in 1992. Additionally, in 1995, plants were grown in the summer months with air conditioning (temperature range= 50-85° F) while the 1992 plants were grown in the greenhouse during the winter months, when temperatures would be much lower, on average. Mean pollen stainability ranged from 7.5 to 91.2% among lines, while mean seed set ranged from 10.8 to 85.7% in 1995. There was no linear relationship between pollen stainability and seed set, based either on individual plants ($b = 0.362$, 223 df), or on entry means ($b = 0.380$, 36 df). Likewise, there was not a linear relationship between pollen stainability and seed set when means were calculated by pedigree ($b = 0.220$, 2 df). Mean pollen stainability and seed set ranged from 54.8 to 85.6% and 29.5 to 35.1%, respectively, when calculated by pedigree (Table 11).

Table 11. Pollen stainability and seed set from 38 primary triticale lines grown in the greenhouse in 1995 at Quincy, Florida, averaged by pedigree.

Pedigree	Pollen stainability (%)	Seed set (%)
CI 14908/GA-Wren's Abruzzi	85.6	29.5
CI 14908/Florida 401	54.8	33.2
CI 14432/Syn-T (4X)	85.2	50.7
Swan 's/Florida 402	74.9	35.1

Chi square values associated with pollen stainability obtained from a heterogeneity analysis, were significant at $P=0.05$ within each of the 38 primary triticale lines

investigated in 1995. Significant chi square values indicate segregation or heterozygosity within lines. Mean comparisons can only be conducted on those means derived from homogeneous entries. Chi square values associated with seed set, significant at $P=0.05$, were also obtained for each of the primary triticale lines except for entries 3, 8, 11, 16, 26, 27, and 29 (Table 12). A one-way analysis of variance was conducted over entries 3, 8, 11, 16, 26, 27 and 29 for mean percent seed set. Entries 27 and 29 had a significantly higher percent seed set than the other entries. Entries 26 and 16 did not have a significantly different seed set percentage although entry 26 did differ from entries 3 and 11 whereas entry 16 did not differ from 3 and 11. Entry 8 had a significantly poorer seed set percentage than the other entries.

Table 12. Mean percent seed set of seven triticale lines grown in the greenhouse in 1995 at Quincy, Florida, in which the chi square values were not significant at $P=0.05$.

1995 greenhouse entry number	Pedigree	Mean seed set [†] (%)
3	CI 14908/GA-Wren's Abruzzi	26.0 c
8	CI 14908/GA-Wren's Abruzzi	10.4 d
11	CI 14908/Florida 401	28.3 c
16	CI 14908/Florida 401	33.2 bc
26	Swan 's'/Florida 402	40.7 b
27	Swan 's'/Florida 402	52.5a
29	Swan 's'/Florida 402	61.0a

[†] Entries followed by the same letter do not differ significantly at $P=0.05$.

Entries 16, 27, and 29 did not have significant seed set heterogeneity, but appeared to be segregating for the "glabrous neck" trait (lack of pubescence on the stem). This segregation gives further evidence that the plants within these lines are the progeny of hybrids and are no longer primary, but secondary triticales.

Micronuclei counts were collected from all plants grown in the greenhouse in 1995 in which the tetrad stage of meiosis could be observed (Fig. 3). Some level of micronuclei were observed in all plants, ranging from fewer than 5%, to more than 88% of quadrants containing one or more micronuclei. Quadrants contained as many as seven micronuclei although the most frequent number observed was one micronuclei per quadrant. Two or three micronuclei were also quite common in some plants, but not as frequent as one.



Fig. 3. Photomicrograph of tetrads containing micronuclei (▲) from primary triticales, 250X magnification.

There was no linear relationship between the percentage of quadrants containing micronuclei and percentage of unstained pollen grains ($b = 0.006$, 201 df).

Hessian Fly Screening for Germplasm Identification

None of the primary triticale lines (entries 1-10) screened at Purdue University in 1996 were uniformly resistant to Hessian fly biotype L (Table 13). Entries 1 and 10 which contain CI 14908 in their pedigrees did have moderate levels of resistance. Several of the F_3 and F_4 generation plants from the primary by secondary crosses did have uniform resistance to Hessian fly biotype L. Differential wheat lines reacted as expected, however, the germplasm Molly, which is resistant to Hessian fly biotype L and contains the H_{13} allele (Patterson et al., 1994), was substituted for Monon which contains the allele H_3 which does not confer resistance to biotype L.

Resistant plants were returned from Purdue University and are being grown in the greenhouse at Quincy, Florida. The most fertile plants derived from lines completely resistant to biotype L are being considered for formal germplasm release in the future. In addition, those plants considered for germplasm release will be tested to identify lines homozygous for biotype E resistance.

Table 13. Triticale screened to Hessian fly biotype L at Purdue University in 1996.

Entry #	Selection	Pedigree	Generation	Reaction (R-S) ¹
1	91PT580-G24-G10-G4(6)	CI 14908/GA-Wren's Abruzzi	C ₅	11-4
2	91PT575-G1-G2-G22(1)	Swan 's'/FL 402	C ₅	6-9
3	91PT575-G1-G8-G23(5)	Swan 's'/FL 402	C ₅	0-14
4	91PT575-G2-G3-G24(1)	Swan 's'/FL 402	C ₅	7-8
5	91PT575-G3-G10-G25(3)	Swan 's'/FL 402	C ₅	5-10
6	91PT575-G3-G4-G27(2)	Swan 's'/FL 402	C ₅	9-5
7	91PT575-G1-G4-G29(1)	Swan 's'/FL 402	C ₅	4-11
8	91PT575-G1-G4-G29(6)	Swan 's'/FL 402	C ₅	5-9
9	91PT575-G4-G10-G30(6)	Swan 's'/FL 402	C ₅	2-12
10	91PT579-G32-PGE1-G35(5)	CI 14908/FL 401	C ₆	13-2
11	(FL201/91PT579-G1)-PGE1-G21	FL201/91PT579-G1	F ₃	10-0
12	(FL201/91PT579-G1)-PGE1-G22	FL201/91PT579-G1	F ₃	12-0
13	(FL201/91PT579-G1)-PGE1-G24	FL201/91PT579-G1	F ₃	5-3
14	(FL201/91PT579-G1)-PGE1-G33	FL201/91PT579-G1	F ₃	13-0
15	(FL201/91PT579-G1)-PGE1-G40	FL201/91PT579-G1	F ₃	13-0
16	(FL201/91PT579-G1)-PGE1-G42	FL201/91PT579-G1	F ₃	13-0
17	(FL201/91PT579-G1)-PGE1-G43	FL201/91PT579-G1	F ₃	9-2
18	(FL201/91PT579-G1)-PGE1-G54	FL201/91PT579-G1	F ₃	9-3

Table 13--continued

Entry #	Selection	Pedigree	Generation	Reaction (R-S)
19	(FL201/91PT579-G1)-PGE1-G55	FL201/91PT579-G1	F ₃	12-0
20	(FL201/91PT579-G1)-PGE1-G61	FL201/91PT579-G1	F ₃	4-0
21	(FL201/91PT579-G1)-PGE1-G62	FL201/91PT579-G1	F ₃	3-10
22	(FL201/91PT579-G1)-PGE1-G70	FL201/91PT579-G1	F ₃	11-0
23	(FL201/91PT579-G1)-PGE1-G72	FL201/91PT579-G1	F ₃	9-0
24	(FL201/91PT579-G1)-PGE1-G73	FL201/91PT579-G1	F ₃	10-1
25	(Sunland/91PT579-G11)-PGE2-G9	Sunland/91PT579-G11	F ₃	13-0
26	(Sunland/91PT579-G11)-PGE2-G14	Sunland/91PT579-G11	F ₃	9-6
27	(Sunland/91PT579-G11)-PGE2-G21	Sunland/91PT579-G11	F ₃	7-3
28	(Sunland/91PT579-G11)-PGE2-G46	Sunland/91PT579-G11	F ₃	9-0
29	(Sunland/91PT579-G11)-PGE2-G50	Sunland/91PT579-G11	F ₃	2-2
30	(Sunland/91PT579-G11)-PGE2-G51	Sunland/91PT579-G11	F ₃	10-1
31	(Sunland/91PT579-G11)-PGE2-G53	Sunland/91PT579-G11	F ₃	7-2
32	(Sunland/91PT579-G11)-PGE2-G56	Sunland/91PT579-G11	F ₃	7-0
33	(Sunland/91PT579-G11)-PGE2-G59	Sunland/91PT579-G11	F ₃	9-0
34	(Sunland/91PT579-G11)-PGE2-G60	Sunland/91PT579-G11	F ₃	5-2
35	(Sunland/91PT579-G11)-PGE2-G65	Sunland/91PT579-G11	F ₃	11-0
36	(Sunland/91PT579-G11)-PGE2-G74	Sunland/91PT579-G11	F ₃	0-6

Table 13--continued.

Entry #	Selection	Pedigree	Generation	Reaction (R-S)
37	(Sunland/9/1PT579-G11)-PGE2-G75	Sunland/9/1PT579-G11	F ₃	9-3
38	(Sunland/9/1PT579-G11)-PGE2-G78	Sunland/9/1PT579-G11	F ₃	8-1
39	(MAH13297-9/9/1PT579-G45)-PGE3-G5	MAH13297-9/9/1PT579-G45	F ₃	6-2
40	(MAH13297-9/9/1PT579-G45)-PGE3-G6	MAH13297-9/9/1PT579-G45	F ₃	7-0
41	(MAH13297-9/9/1PT579-G45)-PGE3-G8	MAH13297-9/9/1PT579-G45	F ₃	7-2
42	(MAH13297-9/9/1PT579-G45)-PGE3-G9	MAH13297-9/9/1PT579-G45	F ₃	8-4
43	(MAH13297-9/9/1PT579-G45)-PGE3-G10	MAH13297-9/9/1PT579-G45	F ₃	13-0
44	(MAH13297-9/9/1PT579-G45)-PGE3-G12	MAH13297-9/9/1PT579-G45	F ₃	11-0
45	(MAH13297-9/9/1PT579-G45)-PGE3-G13	MAH13297-9/9/1PT579-G45	F ₃	9-0
46	(MAH13297-9/9/1PT579-G45)-PGE3-G15	MAH13297-9/9/1PT579-G45	F ₃	8-0
47	(MAH13297-9/9/1PT579-G45)-PGE3-G18	MAH13297-9/9/1PT579-G45	F ₃	10-2
48	(MAH13297-9/9/1PT579-G45)-PGE3-G19	MAH13297-9/9/1PT579-G45	F ₃	4-5
49	(MAH13297-9/9/1PT579-G45)-PGE3-G20	MAH13297-9/9/1PT579-G45	F ₃	3-10
50	(MAH13297-9/9/1PT579-G45)-PGE3-G21	MAH13297-9/9/1PT579-G45	F ₃	11-0
51	(MAH13297-9/9/1PT579-G45)-PGE3-G22	MAH13297-9/9/1PT579-G45	F ₃	10-0
52	(MAH13297-9/9/1PT579-G45)-PGE3-G23	MAH13297-9/9/1PT579-G45	F ₃	11-1
53	(MAH13297-9/9/1PT579-G45)-PGE3-G25	MAH13297-9/9/1PT579-G45	F ₃	9-4
54	(FL201/9/1PT579-G1)-PGE4-G1	FL201/9/1PT579-G1	F ₄	9-0

Table 13--continued.

Entry #	Selection	Pedigree	Generation	Reaction (R-S)
55	(FL201/9IPT579-G1)-PGE4-G2	FL201/9IPT579-G1	F ₄	13-1
56	(FL201/9IPT579-G1)-PGE4-G4	FL201/9IPT579-G1	F ₄	12-0
57	(Sunland/9IPT579-G11)-PGE5-G1	Sunland/9IPT579-G11	F ₄	11-0
58	(Sunland/9IPT579-G11)-PGE5-G4	Sunland/9IPT579-G11	F ₄	13-0
59	(Sunland/9IPT579-G11)-PGE5-G5	Sunland/9IPT579-G11	F ₄	11-0
60	(Sunland/9IPT579-G11)-PGE5-G6	Sunland/9IPT579-G11	F ₄	11-0
61	(Sunland/9IPT579-G11)-PGE5-G7	Sunland/9IPT579-G11	F ₄	12-0
62	(Sunland/9IPT579-G11)-PGE5-G10	Sunland/9IPT579-G11	F ₄	11-0
63	(Sunland/9IPT579-G11)-PGE5-G11	Sunland/9IPT579-G11	F ₄	11-1
64	(Sunland/9IPT579-G11)-PGE5-G12	Sunland/9IPT579-G11	F ₄	12-0
65	(Sunland/9IPT579-G11)-PGE5-G15	Sunland/9IPT579-G11	F ₄	14-0
66	(Sunland/9IPT579-G11)-PGE5-G16	Sunland/9IPT579-G11	F ₄	15-0
67	(Sunland/9IPT579-G11)-PGE5-G18	Sunland/9IPT579-G11	F ₄	8-0
68	(Sunland/9IPT579-G11)-PGE5-G22	Sunland/9IPT579-G11	F ₄	9-0
69	(Sunland/9IPT579-G11)-PGE5-G23	Sunland/9IPT579-G11	F ₄	7-0
70	(Sunland/9IPT579-G11)-PGE5-G25	Sunland/9IPT579-G11	F ₄	14-0
71	(MAH13297-9/9IPT579-G45)-PGE6-G1	MAH13297-9/9IPT579-G45	F ₄	12-0
72	(MAH13297-9/9IPT579-G45)-PGE6-G2	MAH13297-9/9IPT579-G45	F ₄	13-0

Table 13--continued.

Entry #	Selection	Pedigree	Generation	Reaction (R-S)
73	(MAH13297-9/91PT579-G45)-PGE6-G3	MAH13297-9/91PT579-G45	F ₄	13-0
74	(MAH13297-9/91PT579-G45)-PGE6-G4	MAH13297-9/91PT579-G45	F ₄	9-0
75	(MAH13297-9/91PT579-G45)-PGE6-G8	MAH13297-9/91PT579-G45	F ₄	0-7
76	(MAH13297-9/91PT579-G45)-PGE6-G9	MAH13297-9/91PT579-G45	F ₄	14-0
77	(MAH13297-9/91PT579-G45)-PGE6-G10	MAH13297-9/91PT579-G45	F ₄	8-4
78	(MAH13297-9/91PT579-G45)-PGE6-G11	MAH13297-9/91PT579-G45	F ₄	11-0
79	(MAH13297-9/91PT579-G45)-PGE6-G12	MAH13297-9/91PT579-G45	F ₄	14-0
80	(MAH13297-9/91PT579-G45)-PGE6-G14	MAH13297-9/91PT579-G45	F ₄	13-0
81	(MAH13297-9/91PT579-G45)-PGE6-G17	MAH13297-9/91PT579-G45	F ₄	10-0
82	(MAH13297-9/91PT579-G45)-PGE6-G19	MAH13297-9/91PT579-G45	F ₄	7-2
83	(MAH13297-9/91PT579-G45)-PGE6-G20	MAH13297-9/91PT579-G45	F ₄	9-4
84	(MAH13297-9/91PT579-G45)-PGE6-G21	MAH13297-9/91PT579-G45	F ₄	8-4
85	(MAH13297-9/91PT579-G45)-PGE6-G24	MAH13297-9/91PT579-G45	F ₄	9-2
86	(MAH13297-9/91PT579-G45)-PGE6-G28	MAH13297-9/91PT579-G45	F ₄	13-0
87	(MAH13297-9/91PT579-G45)-PGE6-G30	MAH13297-9/91PT579-G45	F ₄	10-0
88	(MAH13297-9/91PT579-G45)-PGE6-G31	MAH13297-9/91PT579-G45	F ₄	2-7
89	(MAH13297-9/91PT579-G45)-PGE6-G33	MAH13297-9/91PT579-G45	F ₄	11-2

Table 13--continued.

Entry #	Selection	Pedigree	Generation	Reaction (R-S)
90	(MAH13297-9/9IPT579-G45)-PGE6-G35	MAH13297-9/9IPT579-G45	F ₄	14-0
91	(MAH13297-9/9IPT579-G45)-PGE6-G36	MAH13297-9/9IPT579-G45	F ₄	12-1
		Differential	Allele	
		Magnum	H ₅	0-53
		Caldwell	H ₆	0-63
		Seneca	H ₇ H ₈	0-48
		Molloy	H ₁₃	68-0

[†]R=resistant, S=susceptible.

CONCLUSIONS

Primary and secondary triticale lines and populations, observed in these studies, have been identified as being resistant to Hessian fly biotypes C, E, and/or L based on seedling screening procedures. Higher than expected levels of susceptibility to these Hessian fly biotypes were observed in all primary triticale lines with CI 14908 in their pedigree. CI 14908 was reported as being resistant to Hessian fly biotypes C, E, and L but was observed as having some susceptibility to biotype C. Since primary triticale, in theory, is homozygous at all loci, no segregation should be observed for Hessian fly resistance, or any other trait, in the absence of partial or complete chromosome loss or addition (aneuploidy). The segregation for Hessian fly resistance in the primary triticale lines might be explained by a number of factors, including: aneuploidy, outcrossing, contamination of Hessian fly biotypes, and misclassification during screening. The two latter factors are the least likely to have been major contributors to the segregation of Hessian fly resistance. All Hessian fly biotypes screened as expected to the differential sets from which they are defined. Additionally, only low levels of misclassification of susceptibility, if any, would be expected by the experienced entomologists at Purdue University. While cytological studies revealed fairly high levels of aneuploidy, as indicated by the presence of micronuclei and chromosome mispairing; very little chromosome deletion was observed in the broad spectrum of primary triticale lines developed in Florida

and Poland. Aneuploidy, as the major cause of segregation of Hessian fly resistance, was not supported by these studies because most primary triticale plants contained the full complement of chromosomes expected by their pedigrees. Outcrossing is probably the most likely reason that the "primary" triticales used in these studies segregated for Hessian fly resistance. If outcrossing was the major contributor to Hessian fly segregation, then the pedigrees of the at least some of the lines used in these studies are in doubt and cannot be determined. Regardless of the pedigree identity, many of these primary triticale lines were observed to have high levels of Hessian fly resistance, to biotypes individually, or in combination. Primary triticale lines, 91PT579-G24, 91PT579-G45, and 91PT579-G47 expressed high levels of resistance to Hessian fly biotype E through two selfpollinated generations and should be considered for release as biotype E resistant germplasm sources. 91PT579-G47 appears to be the most cytologically stable of these three lines.

High levels of resistance to Hessian fly biotypes C and L were observed in several of the secondary triticale lines and cultivars. Both triticale cultivars recently released by the University of Florida (Florida 201 and Sunland) expressed excellent resistance to biotypes C and L as did many of the lines originating from Poland. One line, Trical T89-10, was completely resistant to biotypes C, E, and L. This level of resistance was unexpected in these entries because none were known, specifically, to be Hessian fly resistant. This material, and other triticale germplasm, may be novel sources for Hessian fly resistance that have yet to be fully exploited. Many of the alleles carried in triticale may be unique and could be moved into common wheat with relative ease.

Primary tritcale has many shortcomings, probably the least of which is a possible susceptibility to the Hessian fly. Low fertility and poor seed quality are probably its greatest liability. While a single hybridization with another tritcale appears to partially overcome these poor qualities, multiple hybridization with a broad range of secondary tritcale lines, and strict selection may be necessary to fully recover highly fertile, adapted tritcale with good seed quality. Since secondary tritcale lines and cultivars which are highly resistant to the Hessian fly already exist, it is probably not necessary to resort to the production of primary tritcale to obtain adequate levels of Hessian fly resistance.

Granted, some sources of Hessian fly resistance, such as that obtained from CI 14908, might only be integrated into the tritcale germplasm by the production of primary tritcale if CI 14908 carries unique alleles. These studies were not able to fully characterize the alleles carried by CI 14908 but were able to eliminate several possibilities (H_{10} , H_{11} , H_{12} , H_{14} , H_{17} , H_{19}^+ , and H_{20}). Others were also eliminated as possibilities because they either are not located in the A and B genomes or do not confer resistance to Hessian fly biotype E. Alleles that could not be eliminated as potentially being in common with the biotype E resistance factor(s) in CI 14908 were H_6 , H_9 , H_{15} , H_{16} , and H_{18}^+ .

Even though the Hessian fly resistance carried by CI 14908 could not be fully characterized, it was transferred from this tetraploid wheat source in the formation of primary tritcale. Additionally, this Hessian fly resistance was transferred into, and identified within, secondary tritcale populations via primary by secondary tritcale hybridization. From these studies we have shown that the Hessian fly resistance expressed by CI 14908 is: genetic in nature, transferable by intergeneric hybridization, and transmissible from one generation to the next by sexual reproduction.

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APPENDIX
DATA TABLES

Table A-1. Pollen stainability and fertility data from 1995 summer greenhouse.

'95 greenhouse		Stained pollen	Fertility	'95 greenhouse		Stained pollen	Fertility
Entry ¹	Plant	(%)	(%)	Entry	Plant	(%)	(%)
1	1	83.5	33.3	5	1	81.4	19.7
1	2	88.1	7.6	5	2	89.5	16.7
1	3	93.6	31.9	5	3	96.5	11.7
1	4	93.1	27.0	5	4	85.4	8.5
1	5	92.7	36.8	5	5	86.1	4.1
1	6	85.7	40.8	5	6	73.9	18.1
2	1	91.1	33.7	6	1	80.4	23.5
2	2	92.0	34.8	6	2	94.3	18.7
2	3	91.0	22.4	6	3	86.1	3.2
2	4	96.4	12.4	6	4	90.3	25.1
2	5	79.6	12.7	6	5	92.0	16.2
2	6	96.8	12.1	6	6	80.3	11.0
3	1	87.6	29.0	7	1	75.1	7.6
3	2	91.8	26.0	7	2	84.7	13.5
3	3	77.9	36.7	7	3	88.5	28.2
3	4	76.0	24.6	7	4	95.3	10.0
3	5	86.2	33.3	7	5	92.7	19.4
3	6	91.3	21.6	7	6	90.3	11.7
4	1	86.4	50.0	8	1	90.1	4.5
4	2	88.1	44.4	8	2	82.2	12.7
4	3	77.6	22.4	8	3	86.0	13.5
4	4	92.9	0.0	8	4	79.5	9.0
4	5	96.4	62.4	8	5	75.9	9.0
4	6	87.9	93.3	8	6	95.1	13.5

Table A-1--continued.

'95 greenhouse		Stained pollen (%)	Fertility (%)	'95 greenhouse		Stained pollen (%)	Fertility (%)
Entry	Plant			Entry	Plant		
9	1	88.7	15.2	13	3	74.5	33.3
9	2	76.7	23.1	13	4	94.9	36.0
9	3	81.9	7.7	13	5	54.7	21.5
9	4	73.9	14.3	13	6	95.4	39.4
9	5	76.9	6.8	14	1	81.8	26.3
9	6	93.2	10.5	14	2	51.4	29.9
10	1	94.2	4.8	14	3	73.3	7.3
10	2	75.1	4.8	14	4	59.4	10.6
10	3	38.7	7.4	14	5	9.2	3.5
10	4	86.1	6.2	14	6	0.0	10.6
10	5	69.0	12.3	15	1	82.6	42.9
10	6	89.1	20.0	15	2	86.6	31.9
11	1	92.6	24.7	15	3	71.6	18.1
11	2	86.3	27.9	15	4	87.0	44.8
11	3	91.9	28.5	15	5	95.5	20.1
11	4	93.7	40.5	15	6	87.7	45.2
11	5	86.1	25.0	16	1	85.1	40.8
11	6	82.3	25.2	16	2	94.2	34.1
12	1	93.2	20.7	16	3	2.0	34.7
12	2	0.7	8.0	16	4	0.0	22.7
12	3	0.0	3.2	16	5	94.6	35.3
12	4	87.9	22.8	16	6	83.8	31.3
12	5	40.3	31.1	17	1	23.7	16.9
12	6	70.7	43.7	17	2	94.3	17.8
13	1	5.1	16.7	17	3	1.5	5.0
13	2	68.7	34.9	17	4	2.9	11.6

Table A-1--continued.

'95 greenhouse		Stained pollen	Fertility	'95 greenhouse		Stained pollen	Fertility
Entry	Plant	%	%	Entry	Plant	%	%
17	5	74.1	36.8	22	3	82.9	53.6
17	6	0.0	33.3	22	4	85.7	53.3
18	1	29.2	7.8	22	5	20.4	43.6
18	2	0.5	0.0	22	6	57.8	16.7
18	3	3.2	1.4	23	1	94.6	44.8
18	4	4.5	0.0	23	2	96.9	62.6
19	1	91.4	9.2	23	3	91.3	74.1
19	2	4.8	12.7	23	4	3.4	0.0
19	3	0.0	21.0	23	5	55.5	53.5
19	4	49.9	7.5	23	6	90.7	52.9
19	5	0.0	19.1	24	1	87.1	67.9
19	6	0.0	32.2	24	2	95.2	56.3
20	1	5.5	11.7	24	3	73.1	28.3
20	2	85.8	8.3	24	4	80.3	54.3
20	3	6.0	21.1	24	5	96.4	77.0
20	4	0.0	7.5	24	6	90.2	59.9
20	5	6.3	22.0	25	1	75.7	68.3
20	6	1.9	38.2	25	2	17.7	41.3
21	1	81.8	59.9	25	3	95.2	64.5
21	2	94.8	47.7	25	4	90.2	38.9
21	3	84.1	49.6	25	5	33.2	14.7
21	4	92.5	56.3	25	6	89.8	21.8
21	5	96.9	34.6	26	1	87.9	41.7
21	6	71.1	42.0	26	2	97.1	49.7
22	1	91.7	86.8	26	3	73.1	50.0
22	2	80.4	59.9	26	4	0.5	31.4

Table A-1--continued.

'95 greenhouse		Stained pollen	Fertility	'95 greenhouse		Stained pollen	Fertility
Entry	Plant	(%)	(%)	Entry	Plant	(%)	(%)
26	5	78.1	40.6	31	1	90.1	32.6
26	6	77.4	30.7	31	2	86.2	15.5
27	1	88.8	44.9	31	3	48.1	23.0
27	2	96.4	72.6	31	4	0.9	12.7
27	3	85.6	49.0	31	5	52.6	12.2
27	4	78.4	38.7	31	6	0.0	0.0
27	5	84.4	56.7	32	1	58.3	13.5
27	6	94.0	52.9	32	2	88.7	44.6
28	1	62.6	25.7	32	3	13.4	8.3
28	2	51.4	6.3	32	4	91.7	8.5
28	3	33.8	0.7	32	5	0.0	0.0
28	4	87.9	47.7	32	6	76.6	22.1
28	5	78.5	0.0	33	1	0.0	0.0
28	6	74.3	24.0	33	2	61.7	33.3
29	1	74.1	75.2	33	3	92.8	24.7
29	2	86.7	46.4	33	4	95.0	34.8
29	3	93.0	67.6	33	5	87.9	38.5
29	4	91.7	45.7	33	6	77.8	31.8
29	5	78.5	63.5	34	1	98.4	34.0
29	6	43.9	67.7	34	2	68.2	5.3
30	1	96.3	58.9	34	3	95.1	45.7
30	2	53.3	10.4	34	4	92.9	41.5
30	3	69.5	56.5	34	5	98.1	28.2
30	4	87.6	55.9	34	6	84.3	18.2
30	5	0.0	2.2	35	1	96.5	24.5
30	6	91.9	92.4	35	2	73.0	42.5

Table A-1--continued.

'95 greenhouse		Stained pollen	Fertility	'95 greenhouse		Stained pollen	Fertility
Entry	Plant	(%)	(%)	Entry	Plant	(%)	(%)
35	3	60.6	41.1	37	2	93.2	41.7
35	4	57.3	3.8	37	3	84.7	48.8
35	5	82.9	51.4	37	4	87.0	19.2
35	6	60.2	45.3	37	5	82.5	15.9
36	1	58.6	16.7	37	6	81.1	18.3
36	2	72.9	1.1	38	1	85.2	31.1
36	3	65.8	0.0	38	2	82.5	28.8
36	4	91.8	11.5	38	3	93.9	39.9
36	5	73.7	13.9	38	4	91.5	37.1
36	6	72.8	0.0	38	5	12.6	6.1
37	1	94.6	38.9	38	6	89.0	15.5

†Pedigrees listed in Table 3.

Table A-2. Mitotic chromosome counts and number of cells scored from multiple plants of 38 primary triticales lines grown in the greenhouse in Quincy Florida in 1995.

Greenhouse entry number ¹	Plant	Chromosome number	Number of cells scored
1	1	42	1
1	2	36	3
1	3	42	1
1	4	36	1
1	5		
1	6	42	2
2	1	42	3
2	2	40	2
2	3	28	5
2	4	32	3
2	5	32	2
2	6	42	1
3	1	42	2
3	2	42	1
3	3	36	2
		32	3
3	4	40	1
3	5	42	1
3	6	42	2
4	1	28	4
4	2	42	1
4	3	28	5
4	4	42	2
4	5	42	2
4	6	42	2
5	1	42	3
5	2	42	1
5	3	42	2
5	4	42	3
5	5	42	1
5	6	42	2
6	1	42	2
6	2	42	3
6	3	42	2
6	4	41	1
		38	3
6	5	42	3
6	6	42	2

Table A-2--continued.

Greenhouse entry number	Plant	Chromosome number	Number of cells scored
7	1	42	2
7	2	42	3
7	3	42	2
7	4	42	4
7	5	42	3
7	6	42	1
8	1	42	1
8	2	42	2
		41	2
		40	1
		39	2
8	3	28	3
8	4	42	2
		36	2
8	5	42	1
8	6	42	2
9	1	42	2
9	2	42	2
9	3	42	1
9	4	42	1
		40	2
9	5	42	1
9	6	42	1
10	1	42	3
10	2	42	3
10	3	42	1
10	4	42	2
10	5	42	1
10	6	42	5
11	1	42	3
11	2	42	1
11	3	42	2
11	4	42	2
11	5	42	1
11	6	28	5
12	1	42	2
		38	1
12	2	42	2
12	3	42	1
12	4	42	1

Table A-2--continued.

Greenhouse entry number	Plant	Chromosome number	Number of cells scored
12	5	42	1
12	6	42	2
13	1	42	2
13	2	42	1
		40	2
13	3	42	1
		40	1
13	4	42	2
13	5	42	1
13	6	42	2
14	1	28	4
14	2	42	2
14	3	42	2
14	4	34	4
14	5	34	2
14	6	42	2
15	1	42	3
15	2	42	2
15	3	56	2
		42	1
		44	1
		40	1
		38	2
15	4	42	1
15	5	36	2
15	6	56	3
		42	1
		36	1
16	1	42	2
16	2	42	2
16	3	42	1
16	4	38	1
		34	1
		31	1
16	5	42	1
16	6	42	2
		40	1
17	1	42	2
17	2	42	2
17	3	42	3

Table A-2--continued.

Greenhouse entry number	Plant	Chromosome number	Number of cells scored
17	4	42	2
17	5	42	2
17	6	42	2
18	1	42	3
18	2	34	1
		28	2
18	3	42	1
18	4	42	4
19	1	42	4
19	2	42	2
19	3	42	2
19	4	42	2
19	5	42	2
19	6	42	2
20	1	42	2
20	2	42	1
20	3	42	2
20	4	42	1
20	5	42	1
20	6	42	1
		40	1
21	1	42	3
21	2	42	1
21	3	42	3
21	4	42	1
21	5	42	2
21	6	42	1
22	1	42	2
22	2	42	1
22	3	42	3
22	4	42	2
22	5	42	1
22	6	42	2
23	1	42	3
23	2	42	2
23	3	42	2
		41	1
		40	1
23	4	42	2
23	5	42	3

Table A-2--continued.

Greenhouse entry number	Plant	Chromosome number	Number of cells scored
23	6	42	2
24	1	42	2
24	2	42	2
24	3	42	1
24	4	42	2
24	5	42	1
		84 [†]	2
24	6	42	1
		28	1
25	1	42	3
25	2	42	2
25	3	42	3
25	4	42	2
25	5	42	1
		21	2
25	6	42	3
26	1	36	4
26	2	42	2
26	3	42	2
26	4	42	2
26	5	42	1
26	6	42	2
27	1	42	2
27	2	42	1
27	3	42	1
27	4	42	2
		40	1
27	5	-	1
27	6	42	1
28	1	16	1
		26	2
28	2	42	1
		32	2
		21	1
28	3	42	1
28	4	42	1
		83 [†]	1
28	5	42	2
		38	1
		36	2

Table A-2--continued.

Greenhouse entry number	Plant	Chromosome number	Number of cells scored
28	6	42	2
29	1	42	1
29	2	42	1
		40	2
		38	4
29	3	42	2
29	4	42	1
		41	1
		40	1
29	5	42	3
29	6	42	2
30	1	42	3
30	2	42	2
30	3	42	2
30	4	42	2
30	5	42	1
30	6	38	3
31	1	27	5
31	2	42	2
31	3	42	3
31	4	42	2
31	5	42	1
31	6	42	1
32	1	-	
32	2	42	2
32	3	42	1
		40	1
32	4	42	1
32	5	42	2
		56	1
		55	1
32	6	42	1
33	1	42	2
		27	5
33	2	42	2
33	3	41	2
33	4	-	
33	5	-	
33	6	42	1
		46	1

Table A-2--continued.

Greenhouse entry number	Plant	Chromosome number	Number of cells scored
34	1	42	1
34	2	42	2
34	3	42	1
34	4	42	2
34	5	42	1
34	6	42	2
35	1	42	1
35	2	42	1
35	3	42	2
35	4	42	1
35	5	42	2
35	6	42	1
36	1	-	
36	2	32	1
		28	1
36	3	-	
36	4	-	
36	5	40	1
		32	1
36	6	-	
37	1	42	3
		38	1
		36	2
37	2	42	2
37	3	42	1
37	4	42	2
37	5	42	2
		41	1
37	6	43	2
38	1	22	3
		26	1
38	2	42	1
38	3	42	2
38	4	42	1
38	5	42	1
38	6	42	1

[†]Pedigrees listed in Table 3.[‡] Appeared to be two cells on top of one another.

Table A-3. Cytological observations from 38 primary triticales lines during meiosis, including: number of univalent, bivalent, and tetravalent chromosomes at diakinesis, and chromosome number at anaphase I, anaphase II, and Metaphase II.

1995 greenhouse entry number ¹	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
1	1									
1	2		21	0	2					
1	2		19	4	1					
1	3		21	0	6					
1	3		20	2	2					
1	4									
1	5					21	2			
1	6		21	0	10	21	2			
2	1		21	0	2					
2	2									
2	3									
2	4		21	0	2					
2	5									
2	6		21	0	2					
3	1									
3	2		21	0	2					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
3	2		20	0	2					
3	3		21	0	3					
3	3		19	4	1					
3	4									
3	5		21	0	2					
3	6									
4	1		21	0	15					
4	2									
4	3									
4	4					21	2			
4	5		21	0	2					
4	6									
5	1									
5	2									
5	3		21	0	1					
5	4					21	1			
5	5		21	0	3					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
5	6									
6	1									
6	2									
6	3									
6	4									
6	5			21 0	2					
6	6			21 0	2					
7	1									
7	2			21 0	12					
7	3									
7	4			21 0	3					
7	5									
7	6									21 1
8	1									
8	2									
8	3									
8	4					21	1			

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
8	5							17	2	
8	6									
9	1					21	1			
9	2							21	12	21
9	3									2
9	4									
9	5			21	0	6				
9	6			21	0	5				
9	6			20	2	1				
10	1									
10	2			21	0	10	22	1		
10	2						20	1		
10	3									
10	4			21	0	2				
10	5									21
10	6							21	2	
11	1			21	0	2	21	2		

Table A-3--continued

1995 greenhouse entry number	Plant	Diakinesis		Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells
13	6								
14	1		21	0	19				
14	2								
14	3		21	0	9				
14	4		21	0	7				
14	5		17	0	1				
14	6		21	0	8				
15	1		21	0	4				
15	1		19	4	1				
15	2					28	3		
15	3		28	0	2				
15	3	1	26	0	2				
15	4								
15	5		21	0	1				
15	6		28	0	5				
15	6		27	2	1				
15	6	2	23	2	1				

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
16	1		21	0	22					
16	2		21	0	6					
16	2		20	2	1					
16	3		21	0	5			21		5
16	4		21	0	1					
16	5		21	0	4					
16	5		19	4	1					
16	6		21	0	3					
17	1		21	0	8					
17	2		21	0	7					
17	3		21	0	3					
17	3		19	4	1					
17	4									
17	5							21		2
17	6		21	0	8					
17	6		20	2	2					
17	6		19	4	1					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
18	1		21	0	4					
18	2					17	7			
18	3		21	0	1					21
18	3		20	2	1					2
18	4		21	0	2					
19	1		21	0	8					
19	1		19	4	4					
19	2		21	0	2	21	2			
19	3		21	0	8					
19	4		21	0	3					
19	5		21	0	2					
19	6		21	0	10					
19	6		19	4	1					
20	1		21	0	8					
20	1		20	2	1					
20	1		18	6	1					
20	2		21	0	3					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
20	3		21	0	3					
20	4		21	0	1					
20	5		21	0	8					
20	6		21	0	3					
20	6		20	2	1					
21	1		21	0	4					
21	1		19	4	1					
21	2		21	0	10					
21	3		21	0	1					
21	4		21	0	5					
21	4		17	8	1					
21	5		21	0	2					
21	6		21	0	3					
22	1		21	0	10					
22	1		17	8	2					
22	2		21	0	3					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
24	2					21				
							2			
24	3			21	0					
					9					
24	3			20	2					
					1					
24	3			19	4					
					1					
24	3			18	6					
					1					
24	4			21	0					
					5					
24	5			21	0					
					4					
24	6			21	0					
					5					
25	1			21	0					
					2					
25	2			21	0					
					13					
25	2			20	2					
					2					
25	2			19	4					
					1					
25	3			21	0					
					5					
25	4			21	0					
					4					
25	5			21	0					
					2					
25	6									
26	1			21	0					
					2					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
26	2									
26	3		21	0	2					
26	3		19	4	1					
26	4					21	4			
26	5		21	0	4					
26	5		20	2	1					
26	5		19	4	2					
26	6		21	0	5					
26	6		20	2	1					
27	1									
27	2		21	0	3					
27	3									
27	4									
27	5		21		2					
27	6									
28	1		21		7					
28	1		19	4	1					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
28	1		18	2	I					
28	2									
28	3		21	0	2					
28	4									
28	5									
28	6		21	0	4					
29	1									
29	2									
29	3		21	0	20					
29	3		20	2	2					
29	4		21	0	I					
29	5									
29	6		21	0	3					
30	1		21	0	4					
30	2									
30	3									
30	4		21	0	2					

Table A-3--continued

1995 greenhouse entry number	Plant	Diakinesis				Anaphase I		Anaphase II		Metaphase II	
		IV		I		Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells
		IV	II	I	No. of Cells						
30	5										
30	6										
31	1										
31	2			21 0	1						
31	2			17 0	1						
31	3			21 0	2						
31	4			21 0	2						
31	5										
31	6			21 0	7						
32	1			21 0	12						
32	1			21 2	1						
32	2			21 0	7						
32	3							21	2		
32	4										
32	5										
32	6										
33	1										

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
33	2									
33	3					21				
33	4									
33	5									
33	6									
34	1			21	0	1				
34	2			21	0	7				
34	2			20	2	1				
34	3			21	0	1				
34	4			21	0	7				
34	5			21	0	18				
34	5			20	2	3				
34	5			19	4	1				
34	5			14	14	1				
34	6			21	0	2				
35	1							21	4	
35	2			21	0	1		21	1	

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
35	3									
35	4		21	0	1		18	2		
35	4		19	4	1					
35	5		21	0	10					
35	6									
36	1						16	4		
36	2									
36	3		21	0	12					
36	4									
36	5									
36	6					36	4			
36	6					18	4			
37	1									
37	2									
37	3									
37	4		21	0	4					
37	5		21	0	6					

Table A-3--continued.

1995 greenhouse entry number	Plant	Diakinesis			Anaphase I		Anaphase II		Metaphase II	
		IV	II	I	No. of Cells	Chr. #	No. of Cells	Chr. #	No. of Cells	Chr. #
37	6		21	0	6					
38	1									
38	2		21	0	10					
38	2		19	4	1					
38	2		18	6	1					
38	3		21	0	1	21	3			
38	4		21	0	7					
38	4		20	2	1					
38	4		19	4	1					
38	5		21	0	4	21	1			
38	5		20	2	1	42	1			
38	6									

*Pedigrees listed in Table 3.

Table A-4. Micronuclei analysis of multiple plants of 38 primary triticales lines grown in the greenhouse in Quincy, Florida, in 1995.

1995 greenhouse entry number ¹	Plant	Micronuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
1	1								
1	2	27	50	35	16	6			
1	3	54	60	37	10	2			
1	4								
1	5	47	38	8	1	1	1		
1	6	139	80	24	9	1	1		
2	1	25	2						
2	2								
2	3	120	10	1					
2	4	42	32	6	1	1			
2	5	110	34	15	3				
2	6	87	19	10					
3	1	83	37	19	10	3			
3	2	57	24	10	8	2			
3	3	97	26	6	2	0	1		
3	4	88	46	19	2	1			
3	5	99	28	7	1				
3	6	38	38	27	7	3	2	1	
4	1	74	71	14	1	1			
4	2	104	7						
4	3								
4	4	33	32	17	4	1	0	1	
4	5	83	32	4	2				
4	6								
5	1	89	20	6					
5	2	79	29	11	4	1			

Table A-4-continued

1995 greenhouse entry number	Plant	Micronuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
5	3	45	23	13	3	3			
5	4	64	36	18	3	2			
5	5	105	20	1					
5	6	106	32	35	5				
6	1	119	41	10	1				
6	2	106	32	4	3				
6	3	74	68	15	1				
6	4	95	29	16	3				
6	5	92	49	27	5	1			
6	6	68	27	19	1	1			
7	1	62	32	8	3	2	0	1	
7	2	52	49	12	3				
7	3	102	16	5					
7	4	77	27	12	4	0	1		
7	5	25	44	19	2				
7	6	122	13	3	1				
8	1	101	23	10	2				
8	2	73	24	19	7	2			
8	3	81	23	12	0	1			
8	4	66	11	4	1	1			
8	5	161	83	46	11	3			
8	6	50	28	13	5	0	1		
9	1								
9	2	101	13	3	1				
9	3	101	32	7	3				
9	4	66	13	11	3	1			

Table A 4-continued.

1995 greenhouse entry number	Plant	Microneuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
9	5	79	8	7	4				
9	6	71	24	13	6	0	1		
10	1	76	33	9					
10	2	60	25	17	2				
10	3	63	45	19	2				
10	4	82	33	4					
10	5	101	31	12	3	1			
10	6	45	11	3	2				
11	1	112	18						
11	2	83	16						
11	3	119	23	7					
11	4	112	41	6					
11	5	55	36	11	17				
11	6	79	24	5	1				
12	1	85	15	6					
12	2	84	21	5					
12	3	37	48	15	4	1	1		
12	4	82	58	9	1				
12	5	82	20	6	1				
12	6	86	37	13	2				
13	1	73	75	14	4				
13	2	95	72	11					
13	3	102	25						
13	4	98	14	4	3				
13	5	95	16	12	1	1			
13	6	85	17	3	2	3			

Table A-4--continued.

1995 greenhouse entry number	Plant	Micronuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
14	1	81	24	7	4				
14	2	89	56	14	3	1			
14	3								
14	4	55	58	52	12	2			
14	5								
14	6	71	33	22	5	2	2		
15	1	64	66	28	11	0	2		
15	2	57	32	20	2	4	0	1	
15	3	20	65	55	24	4	4	0	1
15	4	51	50	15	1				
15	5	62	24	24	9	5			
15	6	55	62	15	3				
16	1	67	59	15	1	3			
16	2	76	16	2					
16	3	94	38	24	4				
16	4	53	30	6					
16	5	76	65	25	5				
16	6	79	26	9	1				
17	1	91	10	4	1				
17	2	95	10	9	2				
17	3	75	10	7	2	1			
17	4	99	54	23	4				
17	5	76	12	2	1				
17	6	78	2	1					
18	1	73	8						
18	2	95	60	7					

Table A.4--continued

1995 greenhouse entry number	Plant	Micronuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
18	3	44	27	10	1	1			
18	4	17	36	14	2	0	1		
19	1	106	12	3					
19	2	95	16	6					
19	3	104	5	3					
19	4								
19	5	92	6	1					
19	6	100	20	6					
20	1	78	18	6					
20	2	65	30	5					
20	3	95	16	5					
20	4	76	35	17	0	1	1		
20	5	95	8	3					
20	6	79	35	3	1				
21	1	110	4						
21	2	94	38	1					
21	3	140	9	3					
21	4	89	10	2					
21	5	76	14	3	1				
21	6	92	11	7	1				
22	1								
22	2	125	38	14	5				
22	3	73	33	4	1				
22	4	102	28	15	5	1			
22	5	71	27	8					
22	6	60	70	45	12	4			

Table A.4—continued.

1995 greenhouse entry number	Plant	Micronuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
23	1	113	27	10					
23	2	79	43	17	6				
23	3	104	11	4					
23	4	23	48	31	19	6	2		
23	5	129	32	13	1				
23	6								
24	1	62	17	1					
24	2	106	8	4					
24	3	154	5	1	2	1	1		
24	4	85	21	11	1				
24	5	77	28	6	2				
24	6	73	53	10	1				
25	1	95	18	6					
25	2	51	4	1					
25	3								
25	4	106	23	6	1				
25	5	105	52	2					
25	6								
26	1	76	24	9	3	1			
26	2	117	21	5	2				
26	3	53	28	14	3	0	1	1	
26	4	94	19	1					
26	5	37	19	35	3	1			
26	6	67	35	17	2	2			
27	1	67	29	14	2	0	1		
27	2	110	19	4	0	1			

Table A-4--continued.

1995 greenhouse entry number	Plant	Micronuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
27	3	82	32	5					
27	4	101	42	8	0	1			
27	5	63	16	1					
27	6	99	12	3					
28	1	59	15	10					
28	2	91	25	10					
28	3	86	16	9	1	0	0	1	
28	4	83	17	7	1				
28	5								
28	6	63	56	18	6	3	1		
29	1								
29	2								
29	3								
29	4	87	20	5	1	1			
29	5								
29	6								
30	1	82	23	8	1				
30	2	20	2						
30	3	53	41	21	2	1	1		
30	4								
30	5	9	16	11	2	2			
30	6	58	16	12	2	2			
31	1	73	20	13	1	0	1		
31	2	68	59	8	1				
31	3	95	17	1	2				
31	4	85	27	10					

Table A 4--continued.

1995 greenhouse entry number	Plant	Microneuclei per quadrant (Number of cells observed)							
		0	1	2	3	4	5	6	7
31	5	79	35	9	3				
31	6	111	40	3					
32	1	141	79	57	6	3			
32	2	46	14	4	0	1			
32	3	77	19	6	1				
32	4	68	44	5					
32	5	34	56	41	13	1			
32	6	84	14	5	2	2			
33	1	-							
33	2	109	30	6	2				
33	3	138	32	6	2				
33	4								
33	5	102	16	3	1				
33	6	101	8	8					
34	1	17	14	14	7	1	2		
34	2	17	42	30	42	14			
34	3	111	15						
34	4	41	10	12	5	2	2		
34	5	69	32	7	1	1			
34	6	27	38	18	6	5			
35	1	117	15	7					
35	2	69	76	27	4	2			
35	3	32	14	8	2				
35	4								
35	5	95	61	17	5	1	1		
35	6	54	55	22	7	1	0	1	

Table A.4--continued.

1995 greenhouse		Micronuclei per quadrant							
entry number	Plant	0	1	2	3	4	5	6	7
(Number of cells observed)									
36	1								
36	2	86	52	9	3				
36	3	116	17	9	1				
36	4	31	49	29	10				
36	5	86	79	12	3	3			
36	6	55	31	14	4	1			
37	1	150	12	4					
37	2	94	22	2	1				
37	3	46	14						
37	4	94	34	7	1				
37	5	111	11	2					
37	6	89	37	3	1				
38	1	116	16	5	1				
38	2	90	9	3					
38	3	81	60	10	2	1			
38	4	93	6	4	1				
38	5	186	27	22	3	1			
38	6	91	25	8	1				

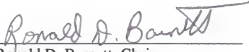
Pedigrees listed in Table 3.

BIOGRAPHICAL SKETCH

Roy Jesse Martens was born in Lovell, Wyoming, on July 10, 1968, and raised on the family farm/ranch. After graduating with honors from Lovell High School in 1986, Roy attended the University of Wyoming in Laramie from which he graduated in August of 1990 with a Bachelor of Science in plant, soil, and insect sciences. He received a Master of Science degree in crop and weed science in May, 1992, from North Dakota State University where he worked on seedling selection traits for sugar beet improvement with the sugar beet research group at the Northern Crop Science Laboratory, USDA-ARS.

Roy began working toward a Doctor of Philosophy degree in agronomy at the University of Florida in August 1992, and is currently a candidate for that degree. Upon completion of his studies, Roy plans to conduct postdoctoral molecular genetic research on hard red spring wheat at Montana State University. Roy eventually wants to work as a plant breeder.

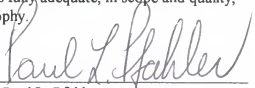
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Ronald D. Barnett, Chair
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Frederick M. Shokes
Professor of Plant Pathology

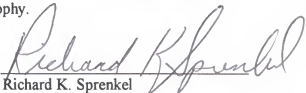
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Paul L. Pfahler
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


David S. Wofford
Associate Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Richard K. Sprenkel
Associate Professor of Entomology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1996


Dean, College of Agriculture

Dean, Graduate School